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A convolute diversity of the *Auriculariales* (*Agaricomycetes, Basidiomycota*) with sphaeropedunculate basidia

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Abstract

Morphological and DNA data show that effused representatives of the *Auriculariales* (Basidiomycota) with sphaeropedunculate basidia belong to eleven genera of which seven are dealt with in this study. Among them, *Myxarium* is the largest genus containing 21 accepted species of which nine are reintroduced below and five are described as new. *Protodontia* is limited to three species only, *P. subgelatinosa* (generic type) and two newly described species from Africa. *Protoacia* is a new monotypic genus for *P. delicata*, sp. nov., widely distributed on coniferous hosts in Eurasia. *Myxariellum* is erected for two new species with smooth hymenophore from northwestern North America while *Gelacantha* is introduced for *G. pura*, a new species with hydnoid hymenophore from Caucasus. Our data do not confirm the present synonymy of *Sebacina sphaerospora* with *Tremella glaira*, and these species are placed in two separate genera – *Hydrophana*, gen. nov., and *Ofella*, gen. nov., respectively.

Keywords: heterobasidiomycetes, internal transcribed spacer, sphaeropedunculate basidium, taxonomy

Introduction

The morphological features of basidia, i.e. their shape, presence of inner septation, and number of sterigmata, remain as cornerstones in basidiomycete taxonomy. Like many other groups recently redefined through DNA-based studies, the *Auriculariales* have included taxa with various basidial morphologies (Weiss & Oberwinkler 2001, Weiss et al. 2004, McLaughlin & Spatafora 2014). Among them, there is a large group of species with a so-called sphaeropedunculate (myxarioid) basidium consisting of a four-celled (rarely two-celled) apical segment and a long enucleate stalk. This kind of basidium was first described by Wells (1964) but its taxonomic applicability was judged in different ways (Donk 1966, Reid 1990, Wells 1994, Roberts 1998). Phylogenetic studies conducted over the last 20 years show that taxa with sphaeropedunculate basidia occur in several, rather distantly related lineages within *Auriculariales* (Weiss & Oberwinkler 2001, Wells et al. 2004, Malysheva et al. 2018, Spirin et al. 2017, 2019). Weiss and Oberwinkler (2001) assumed that the occurrence of this basidial type within a given lineage is constant and, therefore, taxonomically valuable. However, no attempt at a taxonomic revision of taxa with sphaeropedunculate basidia has been undertaken.

In the present paper, we revise the taxonomy of resupinate taxa with sphaeropedunculate basidia, focusing mainly on existing species names and material collected in Europe. A few sequenced collections from North America, East Asia and Africa have been added to our study. In total, five new genera are described, and two exisiting genera, *Myxarium* and *Protodontia*, are redefined.

Material and methods

Morphological study. Specimens from the herbaria H, O, LE, S, C, PC, GB, BPI, K, HBG, NY, FH, TAAM, TU, TRTC, CWU, MA, LY, EA, as well as from the private

collection of the author GT were studied. Herbarium names are abbreviated according to Thiers (2018). Microscopic routine follows Miettinen et al. (2018). All observations and measurements were made from microscopic slides prepared in Cotton Blue, using phase contrast and oil immersion lens (Leitz Diaplan microscope, × 1250 amplification). At least 10 hyphae, 10 basidia and 20 basidiospores were measured for each studied specimen. The following abbreviations are used in morphological descriptions: L – mean basidiospore length, W – mean basidiospore width, Q' – length / width ratio, Q – mean length / width ratio, n – number of measurements per specimens measured.

DNA extraction and sequencing. For DNA extraction, small fragments of dried basidiocarps were used. In total, 58 specimens were selected for molecular sampling (Table 1). DNA was extracted using the NucleoSpin Plant II Kit (Macherey-Nagel GmbH & Co. KG) or High Pure PCR template preparation kit (Roche Applied Science) according to the manufacturer's instructions. PCR amplification and sequencing of the nrITS region was performed using primers ITS1F (Gardes and Bruns 1993), ITSOF (Tedersoo et al. 2008) and ITS4 (White et al. 1990). Primers JS1 (Landvik 1996) and LR5 (Vilgalys and Hester 1990) or LR0R (Hopple and Vilgalys 1994) and LR7 (Vilgalys and Hester 1990) were used to amplify and sequence part of nrLSU region, except LR0R / LR7 products sequenced with CTB6 (Gabrelotto et al. 1998). PCR products were purified applying the GeneJET Gel Extraction Kit (Thermo Scientific, Thermo Fisher Scientific Inc., MA, USA). Sequencing was performed with an ABI model 3130 Genetic Analyzer (Applied Biosystems, CA, USA) and ABI model 3730xl (Macrogen Europe, Amsterdam, Netherlands). Raw data were edited and assembled in MEGA 7 (Kumar et al. 2016). All steps of molecular studies were carried out at the Center for collective use of scientific equipment "Cellular and molecular technology of

studying plants and fungi" (Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg).

Phylogenetic analyses. For this study, 54 nrITS and 48 nrLSU sequences were generated (Table 1). Additionally, 54 nrITS and 51 nrLSU sequences, including the outgroup, were retrieved from GenBank (www.ncbi.nlm.nih.gov/genbank/). Sequences were aligned with the MAFFT version 7 web tool (http://mafft.cbrc.jp/alignment/server/) using the Q-INS-i option for both datasets. Phylogenetic reconstructions were performed with Maximum likelihood (ML) and Bayesian (BA) analyses. Before the analyses, the best-fit substitution model for the alignment was estimated based on the Akaike Information Criterion (AIC) using FindModel web server (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). GTR model was chosen for all datasets.

Maximum likelihood analysis was run on RAxML servers, v.0.6.0 (http://raxml-ng.vital-it.ch/#/) with one hundred rapid bootstrap replicates.

Bayesian analyses was performed with MrBayes 3.2.5 software (Ronquist et al. 2012), for two independent runs, each with 4 million generations under described model and four chains with sampling every 100 generations. To check for convergence of MCMC analyses and to get estimates of the posterior distribution of parameter values, Tracer v1.6 was used (Rambaut et al. 2014). We accepted the result where the ESS (Effective Sample Size) was above 200 and the PSRF (Potential Scale Reduction Factor) was close to 1.

Newly generated sequences have been deposited in GenBank with corresponding accession numbers (Table 1). The alignments have been deposited in TreeBASE (S23483 – ITS+LSU dataset; S23484 – ITS dataset).

Results

Phylogenetic analyses. Two datasets were prepared for the present study: (1) nrITS + nrLSU dataset used to reconstruct a general topology for the *Auriculariales*, with special emphasis on taxa with sphaeropedunculate basidia, and (2) nrITS dataset supporting species concepts in the genus *Myxarium* s.str.

1. nrITS + nrLSU dataset. The final alignment contained 1861 characters (including gaps). The overall topologies of the ML and BI trees were identical and recovered resupinate representatives of the *Auriculariales* with myxarioid basidia in eleven lineages, taxonomically interpreted as genera (Fig. 1). The genus *Hyalodon* is described in detail in Malysheva et al. (2018), *Mycostilla* and *Stypellopsis* are introduced in Spirin et al. (2019). The *Heterochaetella* species characterized by long, thick-walled, tubular cystidia are excluded from this study. The rest of the taxa form seven highly supported clades, only distantly related to each other (Fig. 1):

(A) *Myxarium* covers the largest number of effused taxa with sphaeropedunculate basidia. They are related to *Myxarium nucleatum* Wallr., the genus type, and three other species with cerebriform (exidioid) basidiocarps described in Spirin et al. (2017). *Myxarium crystallinum* D.A. Reid is distantly related to the rest of the species and forms a separate lineage within the large *Myxarium* clade. However, the latter is strongly supported in both ML and BI analyses (bs = 100%, pp = 1), and therefore we keep *M. crystallinum* in *Myxarium*. The generic type of *Microsebacina*, *M. fugacissima* (Bourdot & Galzin) P. Roberts, is revealed as a sister species of *Myxarium podlachicum* (Bres.) Raitv. Most *Myxarium* species dealt with below are distributed in temperate Northern Hemisphere albeit our data point towards a high species diversity also in the tropics.

(B) *Protodontia* represents a separate lineage and encompasses three species, including *P. subgelatinosa* (P. Karst.) Pilát, the generic type. The latter is distributed in the temperate – boreal Northern Hemisphere while two other species are described from tropical areas.

(C) *Hydrophana* is introduced below for *Sebacina sphaerospora* Bourdot & Galzin, a species without close connections with other representatives of the order. The species has been synonymized with *Stypella glaira* (Lloyd) P. Roberts; however, our data show these taxa are not closely related. The single species of *Hydrophana* is so far known from temperate Europe.

(D) *Protoacia* is proposed for a new species, *P. delicata*, from temperate – boreal Eurasia. Morphologically, it is most similar to *Protodontia* spp., although phylogenetically these genera are not closely related.

(E) *Gelacantha* is another new genus introduced for *G. pura*, sp. nov., from the Caucasus. The genus clusters with *Protoacia* and *Tremiscus* Lév. although without strong support.

(F) *Myxariellum*, gen. nov., encompasses two closely related species from northwestern North America described below.

(G) *Ofella* is introduced for *Tremella glaira* Lloyd (= *Stypella glaira*), a rare species from North Europe.

2. nrITS dataset for *Myxarium*. The final alignment contained 758 characters (including gaps). The overall topologies of the ML and BI trees were identical and produced 16 strongly supported clades (Fig. 2). We interpret all of them as taxa of the species rank, with two exceptions:

(A) *Myxarium fugacissimum* is nested within the *Myxarium podlachicum* clade although these species are morphologically clearly different, mainly due to the sessile (not

pedunculate) basidia of the first species. A large infraspecific variation in ITS sequences of *M. podlachicum* may explain why *M. fugacissimum* is not supported as a separate taxon in the ITS phylogeny although it has been recovered as a sister lineage of *M. podlachicum* in the nrITS + nrLSU dataset (Fig. 1). Therefore, we treat these taxa as independent species. The inner variability of *M. podlachicum*, both morphological and genetic, deserves a closer look.

(B) *Myxarium mesomorphum* resolves in the vicinity of *M. nucleatum*, showing 8 bp difference in the ITS region from the latter species. However, one specimen (*Spirin 11760*, treated as *Myxarium* aff. *nucleatum* in Specimens examined) that is morphologically similar to *M. nucleatum* shows a 4 bp difference from *M. mesomorphum* and reveals a more distant relationship to *M. nucleatum* (13 bp difference). Considering sound morphological differences between the latter two, we are unwilling to interpret ITS data as an indication of infraspecific variability. While waiting for a better solution, we accept *M. mesomorphum* and *M. nucleatum* as two separate species. Morphologically, the problematic collection mentioned above comes close to the type of *Exidia alboglobosa* Lloyd described from France and studied by us. More material from temperate Europe and, possibly, other genetic markers are necessary to re-establish its identity.

Morphological diversity. Of the genera described below, *Myxarium* is the most species-rich and morphologically diverse. A minority of its species have cerebriform or addpressed-orbicular, *Exidia*-like basidiocarps: four European species were dealt with in Spirin et al. (2017) and two new species from Africa, *M. frumentaceum* and *M. rotundum*, are added here (Fig. 3a, e, 4c, e, f). The remaining *Myxarium* species possess resupinate basidiocarps; however, their consistency, shape and hymenophore configuration are species-specific and thus crucial for morphological identification. In

particular, fructifications of some species originate as small pustular bodies later partly fusing together but staying discernible in a joint compound basidiocarp (*M. cirratulum*, M. *crystallinum*, *M. grilletii*, *M. minutissimum*) (Fig. 3b, d, g, h). Other species produce effused, continuous basidiocarps with smooth or tuberculate hymenophore (Fig. 3c, f, 4b, d, g, h), except *M. evanidum* and *M. legonii* with spiny hymenial surface (Fig. 4a). All other genera included in this study develop effused, crustaceous basidiocarps. Of them, *Hydrophana*, *Myxariellum* and *Ofella* spp. are smooth, while *Gelacantha*, *Protoacia* and *Protodontia* are (at least partly) hydnoid (Fig. 5).

All taxa treated here are monomitic, with clamped, usually thin-walled hyphae that are poorly differentiated between subiculum and subhymenium. The only exception is *M. crozalcii* which has thick-walled hyphae in the subiculum and very delicate, thin-walled, easily collapsing hyphae in the subhymenium. Hymenial cystidia are characterstic only for *Myxariellum* spp. and they also occur in some specimens of *Myxarium podlachicum* and *Ofella glaira*. *Myxarium fugacissimum* has non-stipitate, sessile basidia, provided with an ansate basal clamp while all other species are characterized by four-celled (more rarely two-celled), subglobose or globose basidia attached to a narrow enucleate stalk.

Ecology. The *Myxarium* species so far known occur on dead wood of angiosperms. Of them, exidioid species (*Myxarium hyalinum* etc.) and effused species with larger basidiocarps (*M. crozalcii*, *M. mesomorphum*) inhabit dead, still attached or recently fallen branches, more rarely small-sized logs of deciduous trees. On the contrary, species with small, resupinate basidiocarps (*M. crystallinum*, *M. evanidum*, *M. fugacissimum*, *M. grilletii*, *M. legonii*, *M. minutissimum*, *M. varium*) are restricted to well-decayed wood remains. *Myxarium podlachicum* often occurs on still corticated but already rather rotten twigs and logs but it can be found also on strongly decomposed

wood. *Hydrophana sphaerospora* prefers excessively moist habitats, especially brook valleys, where it can be detected on various deciduous wood remnants in an advanced decay stage. *Protodontia subgelatinosa* seems to be a ubiquitous although rarely collected species; it has been found in a wide range of habitats, from rich warm-temperate deciduous forests to poor subalpine or subarctic pine-dominated stands. It grows on well-decomposed wood of angiosperms, however. *Ofella glaira* and *Protodontia delicata* have been recorded exclusively on coniferous hosts in intermediate or advanced decay condition. The rest of the taxa presented below are known from a small number of collections, and their ecological preferences require further study.

Taxonomy

Gelacantha V. Malysheva & Spirin, gen. nov.

MB829005

Etymology. From ‘gelum’ (Lat., noun) – frost and ‘acantha’ (Greek, noun) – spine.

Basidiocarps effused, continuous, smooth to irregularly hydnoid, gelatinous, thin. Hyphal structure monomitic; hyphae clamped. Cystidia absent; hyphidia present. Basidia 2–4-celled, 10–12 × 8.5–10 µm, pedunculate. Basidiospores hyaline, thin-walled, ellipsoid to ovoid, 5.5–7 × 4–6 µm. On rotten wood of conifers.

Type species. *Gelacantha pura* V. Malysheva & Spirin.

Gelacantha pura V. Malysheva & Spirin, sp. nov. – Figs. 5a, 6a

Holotype. Russia. Karachaevo-Cherkessia: Karachaevsk Dist, Teberda Nat. Res., *Abies obovata*, 19.VIII.2009 *Malysheva* (LE 254018, isotype – H).

MB829006

Etymology. Purus (Lat., adj.) – pure.

Basidiocarps semitranslucent, effused, continuous, gelatinous, whitish, adnate, drying to a glittering vernicose crust; hymenophore smooth or hydnoid, spines irregularly spread over hymenial surface, acute, up to 150 × 100 μm, often fusing together; subiculum up to 0.1 mm thick, almost invisible in dry condition; margin indistinct; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped, interwoven, subicular hyphae slightly thick-walled, 4–5 μm in diam., subhymenial hyphae thin-walled, 2–3 μm in diam. Cystidia absent; hyphidia abundant, simple to branched, 2–3 μm in diam. at the apical part. Basidia 2–4-celled, (9.2–) 9.8–11.8 (–12.0) × (8.2–) 8.3–10.1 (–10.2) μm (n = 20/1), openly arranged, sometimes obliquely septate; enucleate stalk up to 14 × 4.5 μm, of equal width along the whole length or gradually widening toward apical cells; sterigmata up to 11 × 2.5–4 μm. Basidiospores ellipsoid to ovoid, rarely cylindrical, (5.2–) 5.7–7.2 (–7.3) × (4.1–) 4.2–5.8 (–6.0) μm (n = 30/1), L = 6.45, W = 5.06, Q = 1.28.

Distribution and ecology. Europe (Russian Caucasus); fallen log of *Abies*. So far known from the type locality only.

Remarks. Sparsely and irregularly distributed spines make *G. pura* different from the similar-looking *Protodontia subgelatinosa* and *Protoacia delicata*. The latter species, also occurring on coniferous hosts, has shorter, more globose basidiospores (versus ellipsoid-ovoid in *G. pura*).

Hydrophana V. Malysheva & Spirin, gen. nov.

MB829007

Etymology. From ‘hydor’ (Greek, noun) – water and ‘phaneros’ (Greek, adj.) – apparent.

Basidiocarps effused, continuous, smooth or slightly tuberculate, gelatinous, thin. Hyphal structure monomitic; hyphae clamped. Cystidia absent; hyphidia present. Basidia 4-celled, 7.5–9.5 × 6.5–8.5 μm, pedunculate. Basidiospores hyaline, thin-walled, broadly ellipsoid to subglobose, 4–6 × 3.5–5 μm. On rotten wood of deciduous trees.

Type species. *Sebacina sphaerospora* Bourdot & Galzin.

Hydrophana sphaerospora (Bourdot & Galzin) V. Malysheva & Spirin, comb. nov. – Figs. 5b, 6b, 8

≡ *Sebacina sphaerospora* Bourdot & Galzin, Bull. Soc. Mycol. France 39: 263, 1924. Lectotype. France. Aveyron: Loubotis, *Alnus glutinosa*, 9.IX.1914 *Galzin 16069* (herb. Bourdot 14094) (K(M) 49241, selected by Reid 1973: 296, studied; isolectotype – PC, studied).

= *Myxarium leptocystidiatum* Hauerslev, Mycotaxon 49: 243, 1993. Holotype. Denmark. Hovedstaden: Lyngby-Taarbæk, Ørholm, wood, 9.X.1982 *Hauerslev 6197* (C 19744, studied).

MB829008

Basidiocarps semitranslucent, effused, continuous, smooth or slightly tuberculate, gelatinous, hyaline or greyish, adnate, 0.05–0.2 mm thick, margin indistinct; detectable mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped. Basal hyphae thin-walled, subparallel, 2–2.5 μm in diam.; subhymenial hyphae ascending, thin-walled, glued together, 1–2.2 μm

in diam. Cystidia absent; hyphidia abundant, simple to branched, 0.7–1.5 μm in diam. at the apical part. Basidia 4-celled, (7.3–) 7.7–9.7 (–9.8) × (6.2–) 6.3–8.3 (–8.8) μm (n = 30/3), embedded; enucleate stalk up to 16 × 2–3 μm; sterigmata up to 16 × 1–2 μm. Basidiospores broadly ellipsoid to subglobose, (3.8–) 4.0–6.2 (–6.3) × (3.2–) 3.4–5.2 (–5.3) μm (n = 210/7), L = 4.60–5.22, W = 4.15–4.57, Q = 1.10–1.18.

Distribution and ecology. Europe (Denmark, France, Norway); fallen logs and twigs of deciduous trees in moist places.

Remarks. This species was described as *Sebacina sphaerospora* (Bourdot & Galzin 1924) and later moved to *Myxarium* (Reid 1973). Roberts (1998) suggested that *M. sphaerosporum* is a later synonym of *Stypella glaira* (Lloyd) P. Roberts. However, our data do not confirm these taxonomic replacements and show that *S. sphaerospora* is not closely related to either *Myxarium* spp. or *S. glaira* (= *Ofella glaira* in the present study). Therefore, we have introduced a new genus for it. Morphologically, *H. sphaerospora* is very similar to *Myxarium* spp. except for the small, broadly ellipsoid to subglobose basidiospores. Differences between *H. sphaerospora* and *O. glaira* are more subtle: the latter species has on average longer spores with higher Q values and it occurs exclusively on coniferous hosts.

Myxariellum Spirin & V. Malysheva, gen. nov.

MB829009

Etymology. Myxariellum (Lat., noun) – a deminutive form of *Myxarium*.

Basidiocarps effused, continuous, smooth, gelatinous, very thin. Hyphal structure monomitic; hyphae clamped. Cystidia present, thin-walled, tapering; hyphidia present. Basidia 4-celled, 9–13 × 8–10 μm, pedunculate. Basidiospores hyaline, thin-walled,

broadly ellipsoid to broadly cylindrical, often slightly curved, 5–9.5 × 4–5 µm. On strongly decomposed logs of conifers.

Type species. *Myxariellum concinnum* Spirin & V. Malysheva.

Extremely thin basidiocarps, well-developed cystidia and basidia with thick sterigmata differentiate *Myxariellum* from the other genera treated here.

Myxariellum concinnum Spirin & V. Malysheva, sp. nov. – Figs. 6c, 9

Holotype. USA. Washington: Pend Oreille Co., Sullivan Creek, *Thuja plicata*, 13.X.2014 *Spirin 8393c* (H).

MB829010

Etymology. Concinnus (Lat., adj.) – delicate.

Basidiocarps semitranslucent, effused, continuous, smooth, gelatinous, greyish, adnate, 0.02–0.05 mm thick, margin indistinct; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped, more or less uniform, thin-walled, 1–3 µm in diam. Cystidia scattered, thin-walled, tapering, 15–38 × 6–8.5 µm; hyphidia abundant, simple to sparsely branched, 1–1.5 µm in diam. at the apical part. Basidia 4-celled, (8.2–) 9.1–12.8 (–13.8) × (8.0–) 8.1–9.8 (–10.0) µm (n = 20/1), openly arranged; enucleate stalk up to 11 × 3 µm; sterigmata up to 6–10 × 2–3.5 µm. Basidiospores ellipsoid to broadly cylindrical, often slightly curved, longest spores somewhat fusiform, (6.9–) 7.2–9.7 (–10.2) × (4.0–) 4.1–5.0 (–5.2) µm (n = 30/1), L = 8.31, W = 4.47, Q = 1.87.

Distribution and ecology. North America (United States – Washington); rotten wood of *Thuja*. So far known from the type locality only.

Remarks. Smooth, very thin basidiocarps, well-developed cystidia and rather big, occasionally subfusiform basidiospores differentiate *Myxariellum* from other species included in this study.

Myxariellum tenerum Spirin & V. Malysheva, sp. nov. – Fig. 6d

Holotype. USA. Washington: Pend Oreille Co., Gypsy Meadows, *Picea engelmannii*, 17.X.2014 *Spirin 8685* (H).

MB829011

Etymology. Tener (Lat., adj.) – gentle.

Basidiocarps semitranslucent, effused, continuous, smooth, gelatinous, greyish, adnate, 0.02–0.05 mm thick, margin indistinct; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped, more or less uniform, thin-walled, 1–2 μm in diam. Cystidia scattered, thin-walled, tapering, 24–54 × 6–12 μm; hyphidia abundant, simple to sparsely branched, 1–2 μm in diam. at the apical part. Basidia 4-celled, (8.0–) 9.0–11.8 (–12.0) × (7.2–) 8.0–10.2 (–10.9) μm (n = 20/1), openly arranged; enucleate stalk up to 22 × 2–3 μm; sterigmata up to 7–10 × 2–3.5 μm, occasionally bifurcate. Basidiospores ellipsoid to subglobose, (5.0–) 5.2–6.8 (–7.1) × (4.0–) 4.1–5.0 μm (n = 30/1), L = 5.84, W = 4.58, Q = 1.28.

Distribution and ecology. North America (United States – Washington); rotten wood of *Picea*. So far known from the type locality only.

Remarks. *Myxariellum tenerum* is most similar to *Ofella glaira* in terms of morphology and host preferences but the latter species has thicker basidiocarps and shorter, sparse, poorly developed cystidia. Moreover, distribution areas of these species seem to be different.

Myxarium Wallr., Flora Cryptogamica Germaniae 2: 260, 1833.

Basidiocarps exidioid-cerebriform or effused, pustular-reticulate or continuous, smooth, tuberculate or hydnoid, gelatinous or waxy, in some species with mineral inclusions, mostly small and rather thin. Hyphal structure monomitic; hyphae clamped. Cystidia present in one species, thin-walled, tapering; hyphidia present. Basidia 2–4-celled, 6–18 × 6–12 μm, pedunculate (except one species with sessile basidia). Basidiospores hyaline, thin-walled, broadly ellipsoid or subglobose to narrowly cylindrical, 4–16 × 2.5–7 μm. On wood of deciduous trees.

Type species. *Myxarium nucleatum* Wallr.

Myxarium is the largest genus dealt with in this study. Twelve effused and two exidioid species are described or accepted below, in addition to seven other species (*M. allantosporum*, *M. atratum*, *M. cinnamomescens*, *M. hyalinum*, *M. mesonucleatum*, *M. nucleatum* and *M. populinum*) treated in detail earlier (Kizimova-Horovitz et al. 2000, Wells et al. 2004, Spirin et al. 2017). nrLSU data indicate that the stipitate species *Hyaloria pilacre* and the anamorphic fungus *Helicomyxa everhartioides* (Weiss & Oberwinkler 2001, Kirschner & Chen 2004) are closely related to *Myxarium*. Additional genetic markers are needed to understand their relationships better.

Myxarium cirratulum A. Savchenko & Spirin, sp. nov. – Figs. 3b, 7b

Holotype. Kenya. Taita-Taveta: Taita Hills, Chawia, hardwood branch, 26.XI.2017 *Savchenko 171126/1117* (H7008812).

MB829012

Etymology. Cirratulus (Lat., adj.) – fringed.

Basidiocarps semitranslucent, first pustular with tuft-like apical projections (up to 100 × 40 μm), gelatinous, then fusing together and making a compound reticulate fructification, hyaline to greyish, 0.05–0.1 mm thick, margin indistinct; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped. Basal hyphae indiscernible; subhymenial hyphae ascending, thin-walled, glued together, 2–3 μm in diam. Cystidia absent; hyphidia abundant, sparsely or richly branched, 1–2 μm in diam. at the apical part, covering hymenial surface and forming tuft-like emergences. Basidia mostly 4-celled (rarely 2-celled), (7.8–) 7.9–11.4 (–11.8) × (6.9–) 7.0–8.7 (–9.2) μm (n = 20/1), embedded; enucleate stalk up to 15 × 3 μm; sterigmata up to 15 × 2–3 μm.

Basidiospores ellipsoid to subglobose, (5.1–) 5.2–8.0 (–8.2) × (4.0–) 4.1–5.6 (–6.2) μm (n = 32/1), L = 6.20, W = 4.78, Q = 1.30.

Distribution and ecology. Africa (Kenya); fallen branches of deciduous trees. So far known from the type locality only.

Remarks. *Myxarium cirratulum* is morphologically very close to the European *M. crystallinum* but it has predominantly four-celled basidia. DNA data show that these species are not closely related.

Myxarium crozalcii (Bourdot & Galzin) Spirin & V. Malysheva, comb. nov. – Figs. 3c, 7c, 10

≡ *Sebacina crozalcii* Bourdot & Galzin, Hymén. France: 38, 1928. Lectotype (syntypes). France. Var: Toulon, *Quercus* sp., 2.XII.1925 *Crozalc 23* (herb. Bourdot 40132, PC 0084233), 17.IV.1925 *Crozalc 38* (herb. Bourdot 39065, PC 0084235) (selected by Wells 1961: 360, studied).

= *Heterochaetella bispora* Luck-Allen, Canadian J. Bot. 38: 563, 1960. Holotype. Canada. Ontario: Brant Co., New Durham, *Ulmus* sp., 30.VIII.1937 *Cain* (TRTC 17594).

= *Myxarium stratosum* (Bourdot & Galzin) M. Dueñas, Nova Hedwigia 81: 187, 2005. Lectotype (*Sebacina opalea* f. *stratosa*). Aveyron: St. Sernin, Frégère, *Cerasus* sp., 21.XII.1909 *Galzin 5168* (herb. Bourdot 6916, PC) (selected by Dueñas 2005: 187, studied).

MB829013

Basidiocarps opalescent, effused, continuous, orbicular, from a few mm to 3 cm in diam., waxy, with distinct, white, floccose margin, then opaque, yellowish to ochraceous or brownish, 0.2–1 mm thick; mineral inclusions occasionally present in senescent hymenium, detectable with the naked eye.

Hyphal structure monomitic; hyphae clamped. Basal hyphae subparallel, rather loosely arranged, with distinctly thickened (up to 0.5 μm) walls, (2.0–) 2.1–4.0 (–4.1) μm (n = 40/2), moderately to strongly cyanophilous, some hyphae slightly inflated at septa; subhymenial hyphae ascending, thin-walled, glued together, 1.5–3 μm in diam. Cystidia absent; hyphidia abundant, simple to branched, 1–2 μm in diam. at the apical part. Basidia 4-celled, very rarely 2-celled, (8.1–) 9.2–12.0 (–12.1) × (6.4–) 7.7–9.5 (–9.9) μm (n = 40/4), openly arranged or embedded; enucleate stalk up to 12 × 3 μm, in some basidia strongly reduced; sterigmata up to 12 × 2 μm. Basidiospores broadly cylindrical to cylindrical, slightly curved to almost straight, some spores lacrymoid, 5.8–9.8 (–11.3) × (3.1–) 3.2–5.1 (– 5.8) μm (n = 210/7), L = 6.85–8.71, W = 3.80–4.50, Q = 1.76–2.02.

Distribution and ecology. Europe (France, Germany, Norway, Russia, Spain, Ukraine), Asia (Caucasus – Armenia, East Siberia, Russian Far East), North America (Canada –

Ontario, USA – Iowa); dead, still attached or just fallen, often corticated branches, rarely logs of deciduous trees.

Remarks. Wells (1961) provided detailed information on the type material of *Sebacina crozalcii* and observed the presence of a distinct subiculum consisting of thick-walled generative hyphae. He placed *S. crozalcii* among the synonyms of *Sebacina podlachica*, at that time a collective name for most resupinate *Myxarium* species. From all other species included in this study, *M. crozalcii* differs in having thick, crustaceous basidiocarps with a well-developed subiculum almost unchanging after drying, clearly differentiated subicular hyphae and by its tendency to occur in open, sometimes rather dry habitats. The type material of *Myxarium stratosum* certainly belongs to *M. crozalcii*. The holotype of *Heterochaetella bispora* represents a juvenile specimen of *M. crozalcii* infected by an anamorphic fungus. Hyphal endings of the latter one were mistaken for cystidia in the protologue (Luck-Allen 1960).

Myxarium crystallinum D.A. Reid, Persoonia 7: 293, 1973. – Figs. 3d, 7d

Holotype. United Kingdom. England, Surrey, Ockley, Vann Lake, rotten stump, 22.X.1972 *Reid & Petch* (K(M) 36675, studied).

= *Myxarium gilvum* Hauerslev, Mycotaxon 49: 238, 1993. Holotype. Denmark. Sjælland: Lyngby-Taarbæk, Ørholm, wood, 19.XI.1976 *Hauerslev 5264* (C 19743, studied).

= *Stypella parvula* Hauerslev, Mycotaxon 49: 231, 1993. Holotype. Denmark. Sjælland: Dragør, Kongelunden, wood, 12.X.1980 *Hauerslev 5920* (C 19755, studied).

Basidiocarps translucent, first pustular with tuft-like apical projections (up to 65 × 20 µm), gelatinous, then fusing to a compound, reticulate fructification albeit initial

basidiocarps remain detectable, hyaline to yellowish or pale ochraceous, 0.01–0.04 mm thick, margin indistinct; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped. Basal hyphae indiscernible; subhymenial hyphae ascending, thin-walled, glued together, 1–3 μm in diam. Cystidia absent; hyphidia abundant, sparsely or richly branched, 1–2 μm in diam. at the apical part, spread among basidia but also forming hyphal tufts. Basidia mostly 2-celled, occasionally 4-celled, (6.8–) 7.4–9.3 (–9.4) × (5.8–) 6.1–8.1 (–8.3) μm (n = 20/2), embedded; enucleate stalk up to 19 × 2 μm; sterigmata up to 10 × 2.5–3 μm. Basidiospores broadly ellipsoid to ellipsoid, rarely lacrymoid, (5.6–) 5.8–8.6 (–9.7) × (4.1–) 4.2–6.0 (–6.2) μm (n = 60/2), L = 6.72–7.14, W = 4.92–5.04, Q = 1.34–1.46.

Distribution and ecology. Europe (Denmark, Norway, United Kingdom); strongly rotten wood of deciduous trees (preferably *Ulmus*).

Remarks. *Myxarium crystallinum* is a characteristic species due to the reticulate basidiocarps with tuft-like outgrowths, predominantly 2-celled basidia, and ellipsoid basidiospores. We re-studied the type material of *S. parvula* and concluded it is a later synonym of *M. crystallinum*.

Myxarium evanidum Spirin & K.H. Larss., sp. nov. – Fig. 7e

Holotype. Norway. Møre og Romsdal: Nesset, Eikesdalen, *Ulmus glabra*, 28.IX.2017 *Spirin 11615* (O).

MB829014

Etymology. Evanidus (Lat., adj.) – evanescent.

Basidiocarps semitranslucent, effused, continuous, smooth or indistinctly tuberculate, occasionally producing scattered spine-like outgrowths up to 110 × 70 μm (seen under

lens only!), hyaline to greyish-bluish, sometimes with reddish hue, adnate, 0.03–0.05 mm thick, margin sharply delimited, almost invisible after drying; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped. Basal hyphae sparse, scattered, thin- to slightly thick-walled, 2–2.5 μm in diam.; subhymenial hyphae interwoven or ascending, thin-walled, rather loosely arranged, quickly collapsing, 1.5–2.5 μm in diam. Cystidia absent; hyphidia abundant, branched, 1–2 μm in diam. at the apical part. Basidia 4-celled, (6.3–) 6.4–8.2 (–8.3) × (5.8–) 6.1–7.3 (–7.4) μm (n = 20/1), embedded; enucleate stalk up to 25 × 1.8–2.2 μm; sterigmata up to 15 × 2 μm. Basidiospores broadly cylindrical to cylindrical, often slightly curved, occasionally narrowly ellipsoid, (4.7–) 4.8–7.2 (–7.9) × (2.6–) 2.8–4.3 (–4.8) μm (n = 90/3), L = 5.49–6.72, W = 3.12–3.91, Q = 1.72–1.81.

Distribution and ecology. Europe (Norway); strongly rotten wood of deciduous trees.

Remarks. *Myxarium evanidum* is microscopically very similar to *M. legonii* and *M. minutissimum*. These species can be recognized mostly from their basidiocarp habit: smooth or producing rare hydnoid projections in *M. evanidum*, distinctly hydnoid in *M. legonii* and reticulate in *M. minutissimum*. *Myxarium fugacissimum* is macroscopically most similar to *M. evanidum* but differs by the sessile, non-stipitate basidia.

Myxarium frumentaceum A. Savchenko & V. Malysheva, sp. nov. – Figs. 3e, 7f

Holotype. Kenya. Taita-Taveta: Taita Hills, Chawia forest, hardwood branch, 26.XI.2017 *Savchenko 171126/1400* (H7008816).

MB829015

Etymology. Frumentaceus (Lat., adj.) – frumentaceous.

Basidiocarps semitranslucent, gelatinous, first cerebriform, 1–3 mm in diam., then fusing together, up to 2 cm in widest dimension and 1 mm thick. Margin detaching, later adnate, compact, more or less concolorous with hymenium. Hymenial surface whitish to pale ochraceous, indistinctly furrowed to more or less smooth, in herbarium specimens dark amber to brown. Mineral inclusions abundant, up to 0.3 mm in diam. Hyphal structure monomitic; hyphae clamped. Basal hyphae interwoven, thin-walled, 1.5–2.5 μm in diam., occasionally inflated at septa up to 5–7 μm; subhymenial hyphae ascending, thin-walled, 1–2.5 μm in diam. Cystidia absent; hyphidia abundant, branched, 1–1.5 μm in diam. at the apical part. Basidia (2) 4-celled, (7.7–) 8.0–10.4 (–12.0) × (5.8–) 5.9–7.0 (–7.8) μm (n = 20/1), embedded; enucleate stalk up to 16 × 2–2.5 μm; sterigmata up to 20 × 2 μm. Basidiospores cylindrical, often slightly curved, (6.0–) 6.3–10.1 (–10.2) × (3.1–) 3.2–5.0 (–5.4) μm (n = 60/2), L = 7.38–8.98, W = 3.90–4.32, Q = 1.91–2.09.

Distribution and ecology. Africa (Kenya); fallen hardwood branches.

Remarks. Rather extensive exidioid fructifications and abundant mineral inclusions in mature basidiocarps make *M. frumentaceum* macroscopically indistinguishable from the European species *M. hyalinum* (as reinstated in Spirin et al. 2017). The two species primarily differ by dimensions of basidia and basidiospores, as well as geographic distribution.

Myxarium fugacissimum (Bourdot & Galzin) V. Malysheva & Spirin, comb. nov. – Figs. 3f, 7i

≡ *Sebacina fugacissima* Bourdot & Galzin, Bull. Soc. Mycol. France 25: 28, 1909.

Lectotype. France. Aveyron: St. Estève, *Quercus* sp., 5.V.1915 *Galzin 17914* (herb. Bourdot 14916, PC) (selected by Roberts 1998: 243, studied).

MB829016

Basidiocarps semitranslucent, effused, continuous, smooth or indistinctly tuberculate, hyaline to greyish-bluish, adnate, 0.03–0.1 mm thick, margin sharply delimited; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped. Basal hyphae interwoven, thin-walled, 2–4 μm in diam.; subhymenial hyphae interwoven or ascending, thin-walled, rather densely arranged, 1.5–3 μm in diam. Cystidia absent; hyphidia abundant, branched, 1–2 μm in diam. at the apical part. Basidia 4-celled, (6.3–) 7.0–9.8 (–10.2) × (5.7–) 6.2–8.1 (–9.0) μm (n = 31/4), embedded or openly arranged, sessile, with a large clamp at the base; sterigmata up to 6 × 2 μm. Basidiospores broadly cylindrical to cylindrical, often slightly curved, occasionally narrowly ellipsoid, (5.0–) 5.1–8.1 (–8.2) × (2.3–) 2.5–4.4 (–4.8) μm (n = 120/4), L = 5.89–6.68, W = 3.26–3.68, Q = 1.61–1.93.

Distribution and ecology. Europe (Estonia, France, Norway, Russia), Asia (Russian Far East); strongly rotten wood of deciduous trees.

Remarks. *Myxarium fugacissimum* produces extremely thin basidiocarps on strongly rotten wood of deciduous trees. It is the only *Myxarium* species treated here which has sessile basidia without enucleate stalk. Probably, this feature is connected with the extreme thinness of its fructifications. In our experience, the "zigzag" appearance of subhymenial hyphae described by Wells (1961) and Roberts (1993) as a diagnostic feature of this species is observable only in recent material. Nevertheless, *M. fugacissimum* can be easily identified due to its continuous, thin basidiocarps, non-stipitate basidia provided with a large basal clamp, and small basidiospores.

Myxarium grilletii (Boud.) D.A. Reid, Persoonia 7: 297, 1973. – Figs. 3g, h, 7g, h

≡ *Tremella grilletii* Boud., Bull. Soc. Bot. France 32: 294, 1885. Lectotype. Plate 9, fig. 4 in Bulletin de la Société Botanique de France 32, 1885 (selected here, MBT384909). Epitype. Norway. Oppland: Nord-Fron, Liadalane Nat. Res., *Populus tremula*, 29.IX.2017 *Spirin 11653* (O) (designated here, MBT384910).

Basidiocarps semitranslucent, first small, lenticular or hemispherical, 0.5–1 mm in diam., gelatinous, greyish, sometimes with light violaceous hues, then partly fusing together but remaining discernible, partly detaching, in senescent fructifications coalescent, 0.05–0.5 mm thick; detectable mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped. Basal hyphae indiscernible; subhymenial hyphae ascending, thin-walled, quickly collapsing, 1–3 μm in diam. Cystidia absent; hyphidia abundant, simple to branched, 1–2 μm in diam. at the apical part. Basidia (2) 4-celled, (7.9–) 8.4–10.6 (–10.9) × (6.8–) 6.9–8.8 (–9.8) μm (n = 40/2), embedded; enucleate stalk up to 20 × 2–3 μm; sterigmata up to 20 × 1.5–2 μm. Basidiospores broadly cylindrical to ellipsoid, rarely lacrymoid, (5.2–) 5.3–9.7 (–10.3) × (3.4–) 3.7–5.1 μm (n = 120/4), L = 6.10–7.98, W = 4.15–4.42, Q = 1.47–1.89.

Distribution and ecology. Europe (France, Germany, Norway), Asia (Caucasus – Armenia), North America (Canada – Alberta; USA – Massachusetts); strongly rotten wood of deciduous trees in moist places.

Remarks. The protologue of *Tremella grilletii* accompanied with an illustration of basidiocarps (Boudier 1885) gives a very clear idea of the original species concept. No type material has survived, and the only specimen stored in PC was collected by Boudier in 1903 (https://mnhn.fr) (accessed 25.10.2018). Therefore, we select the original illustration as a lectotype of this species and provide it with an epitype.

Morphologically, *M. grilletii* is most similar to *M. minutissimum* and *M. varium*. The first two species form small hemispherical basidiocarps partly fusing together but they can be separated by basidiospore and basidia dimensions. In turn, basidiospores of *M. varium* are on average narrower than in *M. grilletii*, and it produces continuous fructifications.

Myxarium legonii (P. Roberts) P. Roberts, comb. nov. – Figs. 4a, 7j

≡ *Stypella legonii* P. Roberts, Mycotaxon 69: 228, 1998. Holotype. United Kingdom. England: Surrey, Runnymede, Cooper's Hill, *Ulmus* sp., 5.III.1988 *Legon* (K(M) 49367 – studied)

MB829017

Basidiocarps semitranslucent, effused, continuous, gelatinous, whitish or greyish, adnate; hymenophore hydnoid, spines rather regularly arranged, acute, 0.1–0.6 mm long, 5–7 per mm; subiculum watery greyish, 0.02–0.05 mm thick, almost invisible in dry condition; margin indistinct; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped, more or less uniform, very thin-walled and quickly collapsing, in spines subparallel, 1–2 µm in diam. Cystidia absent; hyphidia abundant, simple to branched, 0.5–1.5 µm in diam. at the apical part. Basidia 4-celled, (6.0–) 6.2–8.2 (–8.8) × (5.0–) 5.2–6.9 (–7.0) µm (n = 40/3), openly arranged; enucleate stalk up to 8 × 2 µm; sterigmata up to 10 × 1–2.5 µm. Basidiospores cylindrical to narrowly ellipsoid, rarely ovoid, (4.1–) 4.2–5.8 (–5.9) × (2.3–) 2.5–3.9 (–4.0) µm (n = 110/4), L = 4.89–5.28, W = 2.94–3.25, Q = 1.51–1.81.

Distribution and ecology. Africa (Malawi), Europe (Russia, United Kingdom), North America (Canada – Alberta, United States – New York, Tennessee); strongly rotten wood of deciduous trees.

Remarks. *Myxarium legonii* is the only truly hydnoid species so far assigned to the genus. Macroscopically, it is most similar to *Protodontia subgelatinosa*, which differs in having broader, ellipsoid basidiospores and larger basidia. ITS sequences of *M. legonii* are considerably variable and the American specimens so labelled may turn out to represent yet another species. They are morphologically indistinguishable from the European material we studied, however.

Myxarium mesomorphum (Bourdot & Galzin) Hauerslev, comb. nov. – Figs. 4b, 7k

≡ *Sebacina mesomorpha* Bourdot & Galzin, Bull. Soc. Mycol. France 39: 262, 1924.

Lectotype. France. Aveyron: Boutaran, *Rosa canina*, 12.V.1914 *Galzin 15287* (herb. Bourdot 13949, PC) (selected by Hauerslev 1993: 245, studied).

MB829019

Basidiocarps semitranslucent, effused, continuous, smooth or tuberculate, hyaline to greyish-bluish, adnate, 0.1–0.3 mm thick, margin sharply delimited, older basidiocarps with ochraceous or vinaceous-brownish tints; mineral inclusions occasionally present in senescent basidiocarps, detectable under lens only.

Hyphal structure monomitic; hyphae clamped. Basal hyphae observable only in the thickest basidiocarps, thin- to slightly thick-walled, interwoven, 2.8–4 μm in diam.; subhymenial hyphae ascending, thin-walled, rather loosely arranged, quickly collapsing, 1.5–3 μm in diam. Cystidia absent; hyphidia abundant, branched, 1–1.5 μm in diam. at the apical part. Basidia 2–4-celled, (10.2–) 10.3–14.3 (–15.2) × (8.3–) 9.0–11.2 (–12.8)

µm (n = 30/3), embedded; enucleate stalk up to 31 × 2–3 µm; sterigmata up to 39 × 2 µm. Basidiospores broadly cylindrical to cylindrical, straight or slightly curved, occasionally ellipsoid-lacrymoid, (8.9–) 9.1–14.7 (–15.8) × (4.1–) 4.2–7.2 (–7.3) µm (n = 160/6), L = 10.54–12.11, W = 4.95–5.71, Q = 1.94–2.24.

Distribution and ecology. Europe (Denmark, Finland, France, Norway, Russia); still attached dead or recently fallen, often corticated branches of deciduous trees.

Remarks. Hauerslev (1993) reintroduced this species based on authentic material and other collections from temperate Europe. However, the combination he proposed is technically invalid (due to imcomplete basionym's citation), and therefore we validate it here. Wells (1961) considered *Sebacina mesomorpha* a synonym of *Exidiopsis laccata* (Bourdot & Galzin) Luck-Allen. Our study does not support this view and the identity of the latter species will be clarified on a later occasion.

Myxarium mesomorphum is easily recognizable due to its rather extensive, resupinate basidiocarps occurring on hardwood branches. It can be confused with coalescent fructifications of *M. hyalinum*; however, the latter are strongly tuberculate and contain large mineral inclusions easily visible with the naked eye. Old, fused fructifications of *M. cinnamomescens* may also be mistaken for vigorously growing specimens of *M. mesomorphum*; however, they are normally thicker and pulvinate in *M. cinnamomescens* (Fig. 3a). Moreover, basidiospores of *M. cinnamomescens* are in general long cylindrical and narrower (Fig. 7a) although mean width values are overlapping with those of *M. mesomorphum*.

Myxarium minutissimum (Höhn.) Spirin & Trichies, comb. nov. – Figs. 7l, 11

≡ *Exidia minutissima* Höhn., Ann. Mycol. 2: 38, 1904.

= *Tremella glacialis* Bourdot & Galzin, Bull. Soc. Mycol. France 39:261, 1924. Lectotype. France. Gironde: Bordeaux, *Populus*, X.1915 *Galzin 18518* (K(M) 48787, studied) (selected by Reid 1973: 295).

MB829020

Basidiocarps semitranslucent, hardly detectable, first pustular, gelatinous, 0.05–0.1 mm in diam., then fusing together and producing a compound reticulate fructification, hyaline or light greyish, 0.03–0.1 mm thick, margin indistinct; detectable mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped. Basal hyphae thin- to only slightly thick-walled, parallel, 2.5–4 μm in diam., in older basidiocarps indiscernible; subhymenial hyphae ascending, thin-walled, glued together, 1–2.5 (3) μm in diam. Cystidia absent; hyphidia abundant, simple to branched, 1–2 μm in diam. at the apical part. Basidia 4-celled, (6.3–) 6.8–10.1 (–10.2) × (6.0–) 6.1–7.8 (–8.0) μm (n = 70/5), openly arranged or embedded; enucleate stalk up to 22 × 2 μm; sterigmata up to 27 × 1.5–2 μm. Basidiospores broadly cylindrical to cylindrical, slightly curved to almost straight, more rarely narrowly ellipsoid, (4.9–) 5.1–8.1 (–8.3) × (2.7–) 2.9–4.2 (–4.4) μm (n = 150/5), L = 5.79–7.25, W = 3.26–3.71, Q = 1.72–1.98.

Distribution and ecology. Europe (Austria, France, Norway, Russia); strongly rotten wood of deciduous trees.

Remarks. The protologue of *Exidia minutissima* (Höhnel 1904) is very clear and stresses such important characters as tiny, pustulate, partly fusing basidiocarps and small basidiospores. Unfortunately, no type material has been available for our study, and Höhnel's original collection seems to be lost. If further search for it in Vienna should be unsuccessful, a neotype should be selected to maintain the current species concept.

From the similar-looking *M. grilletii*, another European species with compound, reticulate basidiocarps, *M. minutissimum* can be differentiated by considerably more narrow basidiospores and by slightly smaller basidia. The recently described *M. grilletii* f. *invisibile* (Gaignon et al. 2015) seems to refer to a juvenile, pustulate stage of *M. minutissimum*. We did not find any essential microscopic differences between the type of that form and other specimens of *M. minutissimum* studied by us. Unfortunately, our attempts to sequence *M. grilletii* f. *invisibile* were unsuccessful.

Myxarium podlachicum (Bres.) Raitv., Plants and Animals of the Far East: 113, 1971. – Figs. 4d, 7m

≡ *Sebacina podlachica* Bres., Ann. Mycol. 1: 117, 1903. Lectotype. Poland. Mazovia, *Betula* sp., *Eichler 63* (S F21173, studied) (selected by Roberts 1998: 224).

= *Sebacina subhyalina* A. Pearson, Trans. British Mycol. Soc. 13: 71, 1928. Lectotype. United Kingdom, England, East Sussex, Buckhurst Wood, *Fagus sylvatica*, 30.X.1926 *Pearson* (K(M) 48327, studied) (selected by Reid 1970: 426)

= *Sebacina sublilacina* G.W. Martin, Mycologia 26: 262, 1934.

= *Myxarium vernicosum* Hauerslev, Mycotaxon 49: 253, 1993.

Basidiocarps semitranslucent, effused, continuous, smooth or indistinctly tuberculate, hyaline to greyish-bluish, sometimes with light violaceous hues, adnate, 0.1–0.5 mm thick, margin sharply delimited, older basidiocarps with ochraceous or vinaceous-brownish tints; mineral inclusions present in senescent basidiocarps, often abundant, observable with the naked eye.

Hyphal structure monomitic; hyphae clamped. Basal hyphae observable only in young basidiocarps, thin- to slightly thick-walled, subparallel, 2–4 μm in diam.; subhymenial

hyphae interwoven, thin-walled, densely glued together, 1.5–3 μm in diam. Cystidia present in some specimens, often subulate to carrot-shaped, rarely clavate, 14–34 × 3–6 μm; hyphidia abundant, branched, 1–3 μm in diam. at the apical part. Basidia 4-celled, (8.2–) 8.3–11.0 (–11.8) × (6.4–) 6.8–9.3 (–9.8) μm (n = 40/3), openly arranged or embedded; enucleate stalk up to 13 × 2–3 μm; sterigmata up to 25 × 2–3 μm. Basidiospores broadly cylindrical to cylindrical, often slightly curved, (5.6–) 5.8–10.1 (–10.2) × (3.0–) 3.1–5.1 (–5.2) μm (n = 210/7), L = 6.75–8.61, W = 3.59–4.38, Q = 1.86–1.97.

Distribution and ecology. Europe (Denmark, Finland, Germany, Norway, Poland, Russia, United Kingdom), North America (Canada – Alberta, Ontario); rotten wood (logs and branches) of deciduous trees in various habitats.

Remarks. We re-studied a lectotype of *Sebacina podlachica* and found that it belongs to an effused species with continuous basidiocarps, interwoven subhymenial hyphae and subulate cystidia. These features make it an older name for *M. subhyalinum*. Therefore, the present synonymy of *S. podlachica* with *M. grilletii* should be abandoned. The appropriate combination of *S. podlachica* in *Myxarium* was already proposed by Raitviir (1971).

Cystidia are hardly discernible in senescent basidiocarps of *M. podlachicum*. Nevertheless, these fructifications are identifiable due to tightly interwoven and strongly gelatinized hyphae and the presence of abundant mineral inclusions easily visible with the naked eye. *Myxarium podlachicum* is one of the most common species in the genus, occurring in temperate and boreal forests.

Myxarium rotundum A. Savchenko & Spirin, sp. nov. – Figs. 4f, 7n

Holotype. Kenya. Taita-Taveta: Taita Hills, Chawia, hardwood branch, 27.XI.2017 *Savchenko 171127/1025* (H7008825).

MB829021

Etymology. Rotundus (Lat., adj.) – roundish.

Basidiocarps semitranslucent, adpressed-orbicular, hyaline to greyish, adnate, 0.4–2 mm in diam., 0.2–0.5 mm thick, first solitary, then partly fusing together; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped. Tramal and subhymenial hyphae ascending, thin-walled or with distinct walls, rather loosely arranged, 1–2 μm in diam., occasionally bearing ampullaceous septa and then up to 5 μm in diam. Cystidia absent; hyphidia abundant, branched, 1–1.5 μm in diam. at the apical part. Basidia 4-celled, (8.8–) 9.4–11.3 (–11.4) × (7.3–) 8.0–9.4 (–10.4) μm (n = 20/1), openly arranged or embedded; enucleate stalk up to 33 × 2–3 μm; sterigmata up to 30 × 2 μm. Basidiospores broadly cylindrical to cylindrical, sometimes slightly curved, (7.2–) 7.5–10.2 (–10.3) × (3.5–) 3.7–5.0 (–5.1) μm (n = 30/1), L = 8.96, W = 4.25, Q = 2.12.

Distribution and ecology. Africa (Kenya); fallen branch of deciduous tree. So far known from the type locality only.

Remarks. Small-sized, orbicular basidiocarps and short basidiospores differentiate *M. rotundum* from the other exidioid species in the genus.

Myxarium simile A. Savchenko & V. Malysheva, sp. nov. – Figs. 4g, 7o

Holotype. Kenya. Taita-Taveta: Taita Hills, Mbololo forest, hardwood branch, 29.XI.2017 *Savchenko 171129/1120A* (H7008869).

MB829022

Etymology. Similis (Lat., adj.) – similar.

Basidiocarps semitranslucent, effused, continuous, distinctly tuberculate, hyaline to greyish-bluish, adnate, 0.3–0.5 mm thick, margin sharply delimited; mineral inclusions abundant, detectable with the naked eye.

Hyphal structure monomitic; hyphae clamped. Basal hyphae indiscernible; subhymenial hyphae ascending, thin-walled, rather loosely arranged, 1.5–2 μm in diam. Cystidia absent; hyphidia abundant, branched, 0.5–1 μm in diam. at the apical part. Basidia 4-celled, (7.8–) 8.0–9.8 (–10.2) × (6.9–) 7.0–8.3 (–8.4) μm (n = 20/1), embedded; enucleate stalk up to 20 × 2–2.5 μm; sterigmata up to 23 × 1.5–2 μm. Basidiospores broadly cylindrical to cylindrical, sometimes slightly curved, (5.7–) 5.8–7.3 × (3.0–) 3.1–4.1 (–4.2) μm (n = 30/1), L = 6.59, W = 3.47, Q = 1.92.

Distribution and ecology. Africa (Kenya); living angiosperm tree. So far known from the type locality only.

Remarks. The effused, continuous basidiocarps of *Myxarium simile* containing numerous, well-visible mineral grains are strongly reminiscent of *M. podlachicum*, which, however, possesses interwoven, densely arranged subhymenial hyphae and occasional cystidia. Another look-alike, *Myxarium varium*, is devoid of mineral inclusions and it has on average longer basidiospores and larger basidia.

Myxarium varium Hauerslev, Mycotaxon 49: 253, 1993. – Figs. 4h, 7p, 12

Holotype. Denmark. Sjælland: Faxe, Vemmetofte Skov, wood, 23.IX.1977 *Hauerslev 6097* (C 19746, studied).

Basidiocarps semitranslucent, effused, continuous, tuberculate, gelatinous, greyish, sometimes with light violaceous hues, adnate, drying to hardly visible ochraceous or brownish crust, 0.05–0.2 mm thick, margin indistinct; mineral inclusions absent. Hyphal structure monomitic; hyphae clamped. Basal hyphae with thin but distinct walls, 2–3 μm in diam., quickly collapsing, rarely inflated at septa up to 4–6 μm; subhymenial hyphae ascending, thin-walled, 1.5–2 μm in diam. Cystidia absent; hyphidia abundant, simple to branched, 1–2 μm in diam. at the apical part. Basidia 2–4-celled, (7.8–) 7.9–11.2 (–12.8) × (6.3–) 6.4–9.0 (–9.3) μm (n = 60/6), often embedded; enucleate stalk up to 20 × 2–3 μm; sterigmata up to 25 × 1.5–2.5 μm. Basidiospores broadly cylindrical to cylindrical, often slightly curved, rarely narrowly ellipsoid, (6.0–) 6.1–9.8 (–10.2) × (2.8–) 2.9–4.5 (–4.8) μm (n = 180/6), L = 7.07–8.13, W = 3.41–4.01, Q = 1.91–2.16.

Distribution and ecology. Europe (Denmark, Estonia, Finland, France, Germany, Norway, Russia, Sweden); strongly rotten wood of deciduous trees in various habitats.

Remarks. *Myxarium varium* is morphologically very close to *M. grilletii* and differs mainly by having continuous (not lenticular-compound) basidiocarps. The presence of inflated hyphal segments stressed as diagnostic in the protologue of *M. varium* (Hauerslev 1993) is inconstant, and therefore this feature alone cannot be used for morphology-based identification.

Ofella Spirin & V. Malysheva, gen. nov.

MB829023

Etymology. Ofella (Lat., noun) – a tiny piece.

Basidiocarps effused, continuous, smooth or slightly tuberculate, gelatinous, thin. Hyphal structure monomitic; hyphae clamped. Cystidia occasionally present,

embedded; hyphidia present. Basidia 4-celled, 8–10.5 × 7.5–10 μm, pedunculate. Basidiospores hyaline, thin-walled, ellipsoid or broadly ellipsoid to subglobose, 5–8 × 4–5 μm. On rotten wood of coniferous trees.

Type species. *Tremella glaira* Lloyd.

Ofella glaira (Lloyd) Spirin & V. Malysheva, comb. nov. – Figs. 6e, 13

≡ *Tremella glaira* Lloyd, Mycol. Writings 5: 874, 1919. Lectotype. Sweden. Småland: Femsjö, *Pinus sylvestris*, 1909 *Lloyd* (BPI 702239, studied) (selected by Wells 1961: 332).

MB829024

Basidiocarps semitranslucent, effused, smooth or slightly tuberculate, gelatinous, cream to pale ochraceous, adnate, 0.1–0.2 mm thick, in dry condition partly detaching, sometimes with scattered crater-like holes, margin indistinct; mineral inclusions absent. Hyphal structure monomitic; hyphae clamped, more or less uniform, interwoven, thin-walled, 1.5–3 μm in diam. Cystidia occasionally present, 16–40 × 4.5–8 μm, normally embedded; hyphidia abundant, simple to sparsely branched, 1–2.5 μm in diam. at the apical part. Basidia 4-celled, (7.8–) 8.0–10.6 (–10.7) × (7.0–) 7.3–9.8 (–10.5) μm (n = 40/2), openly arranged; enucleate stalk up to 22 × 2–3 μm; sterigmata up to 25 × 1.5–2.5 μm. Basidiospores ellipsoid or broadly ellipsoid to subglobose, (4.6–) 4.8–8.1 (–8.8) × (4.0–) 4.1–5.3 (–5.8) μm (n = 90/3), L =5.92–6.98, W = 4.63–4.73, Q = 1.28–1.48.

Distribution and ecology. Europe (Estonia, Finland, Norway, Sweden); strongly rotten wood of conifers (*Picea, Pinus*).

Remarks. *Ofella glaira* is a very rare species, so far detected only in North Europe. It differs from *Gelacantha pura* and *Protoacia delicata* in having a completely smooth

hymenophore. *Hydrophana sphaerospora* has shorter, more rounded basidiospores and occurs exclusively on angiosperms.

Protoacia Spirin & V. Malysheva, gen. nov.

MB829026

Etymology. From ‘protos’ (Greek, adj.) – primal and ‘acus’ (Lat., noun) – needle.

Basidiocarps effused, continuous, gelatinous, thin, hymenophore hydnoid, spines up to 1 mm long. Hyphal structure monomitic; hyphae clamped, very thin-walled, easily collapsing. Cystidia absent; hyphidia present. Basidia 4-celled, 7.5–10.5 × 6–9 μm, pedunculate. Basidiospores hyaline, thin-walled, broadly ellipsoid to subglobose, 5–6.5 × 4–5.5 μm. On strongly decomposed logs of conifers.

Type species. *Protoacia delicata* Spirin & V. Malysheva.

Protoacia delicata Spirin & V. Malysheva, sp. nov. – Figs. 5c, 6f, 14

Holotype. Russia. Leningrad Reg.: Boksitogorsk Dist., Chagoda, *Picea abies*, 24.IX.2011 *Spirin 4615* (H).

MB829027

Etymology. Delicatus (Lat., adj.) – delicate.

Basidiocarps semitranslucent, effused, gelatinous, whitish or watery greyish, adnate; hymenophore hydnoid, spines more or less regularly arranged, acute, 0.2–0.8 mm long, 5–6 per mm; subiculum whitish or watery greyish, 0.05–0.2 mm thick, drying to vernicose, partly detaching crust; margin sharply delimited; mineral inclusions absent. Hyphal structure monomitic; hyphae clamped, more or less uniform, very thin-walled, easily collapsing, in spines subparallel, 2–3.5 μm in diam. Cystidia absent; hyphidia

abundant, simple to branched, 1–3 µm in diam. at the apical part. Basidia 4-celled, (7.3–) 7.7–10.7 (–11.0) × (5.9–) 6.2–8.8 (–8.9) µm (n = 31/3), openly arranged; enucleate stalk up to 28 × 3 µm; sterigmata up to 8–15 × 2–3 µm. Basidiospores broadly ellipsoid to subglobose, rarely broadly ovoid, (4.7–) 4.8–6.8 (–7.0) × 4.1–5.8 (–5.9) µm (n = 120/4), L = 5.30–5.96, W = 4.72–5.11, Q = 1.10–1.19.

Distribution and ecology. Europe (Norway, Russia, Sweden), Asia (Russian Far East); strongly rotten wood of conifers, mostly *Picea*.

Remarks. *Protoacia delicata* is a characteristic species due to its distinctly hydnoid hymenophore and occurrence on coniferous hosts. The similar-looking *Protodontia subgelatinosa* differs in having longer, ellipsoid-ovoid basidiospores and it grows on wood of deciduous trees. *Gelacantha pura* has ellipsoid basidiospores too, but it possesses scattered, irregularly arranged outgrowths on the hymenial surface. *Hyalodon* spp. have longer spines, densely packed tramal hyphae with thickened walls and on average narrower, mostly broadly ellipsoid basidiospores.

Protodontia Höhn., Sitz. Kaiserl. Akad. Wiss. Math.-naturwiss. Klasse Abt. I 116: 83, 1907.

Basidiocarps effused, continuous, gelatinous, thin; hymenophore minutely denticulate to hydnoid. Hyphal structure monomitic; hyphae clamped, thin- or only slightly thick-walled. Cystidia absent; hyphidia present. Basidia 4-celled, 8.5–11 × 7.5–10.5 µm, pedunculate. Basidiospores hyaline, with distinct wall, broadly ellipsoid to subglobose, 5–9 × 4–6 µm. On strongly decomposed wood of deciduous trees.

Type species. *Protodontia uda* Höhn.

The genus is limited here to three species, *P. subgelatinosa* from temperate Eurasia and two African species. Our study confirms that *Protodontia filicina* Parmasto is a later synonym of *Hyalodon piceicola* (Kuehner) V. Malysheva & Spirin (= *Protohydnum piceicola* Kuehner ex Bourdot) while *P. oligacantha* G.W. Martin with non-stipitate basidia will be dealt with on another occasion.

Protodontia africana A. Savchenko & Spirin, sp. nov. – Fig. 6g

Holotype. Kenya. Taita-Taveta: Taita Hills, Chawia, hardwood branch, 26.XI.2017 *Savchenko 171126/1104* (H7008811).

MB829028

Etymology. Africanus (Lat., adj.) – African.

Basidiocarps semitranslucent, effused, gelatinous, whitish or greyish, adnate; hymenophore minutely denticulate, spines regularly arranged, sometimes fusing in groups of 2–3, acute, 0.2–0.3 mm long, 3–4 per mm; subiculum watery greyish, 0.04–0.1 mm thick, almost invisible in dry condition; margin indistinct; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped, more or less uniform, thin- or only slightly thick-walled, in spines subparallel, 2–3.5 μm in diam. Cystidia absent; hyphidia rare, sparsely branched, 1–1.5 μm in diam. at the apical part. Basidia 4-celled, (7.3–) 7.8–10.3 (–11.0) × (6.2–) 6.8–8.4 (–8.8) μm (n = 20/1), openly arranged; enucleate stalk up to 16 × 2–3 μm; sterigmata up to 6 × 2.5–3 μm, occasionally branched.

Basidiospores broadly ellipsoid to subglobose, (4.7–) 4.9–6.3 (–7.3) × (3.9–) 4.0–5.1 (–5.2) μm (n = 30/1), L = 5.51, W = 4.53, Q = 1.22.

Distribution and ecology. Africa (Kenya); fallen branch of deciduous tree. So far known from the type locality only.

Remarks. Of the three *Protodontia* species accepted here, *P. africana* has the smallest basidiospores. Regularly arranged and longer spines differentiate it from *P. insularis*.

Protodontia insularis Spirin & V. Malysheva, sp. nov. – Fig. 6h

Holotype. St. Helena. Diana Peak Nat. Park, hardwood, 2.II.2014 *Ryvarden 49417* (H, isotype – K).

MB829029

Etymology. Insularis (Lat., adj.) – insular.

Basidiocarps semitranslucent, effused, gelatinous, whitish or greyish, adnate; hymenophore minutely denticulate, spines irregularly arranged, sometimes fusing in groups of 2–3, acute, 0.02–0.1 mm long, 3–5 per mm; subiculum watery greyish, 0.02–0.03 mm thick, almost invisible in dry condition; margin indistinct; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped, more or less uniform, thin- or only slightly thick-walled, in spines subparallel, 1.5–2.5 μm in diam. Cystidia absent; hyphidia rare, simple to branched, 1–1.5 μm in diam. at the apical part. Basidia 4-celled, (7.8–) 8.3–10.8 (–11.3) × (7.1–) 7.7–9.2 (–9.3) μm (n = 20/1), openly arranged; enucleate stalk up to 8 × 2–3 μm; sterigmata up to 5 × 2.5–3 μm. Basidiospores broadly ellipsoid to subglobose, (5.1–) 5.2–7.1 (–7.2) × (4.1–) 4.2–5.5 (–5.8) μm (n = 30/1), L = 5.97, W = 4.82, Q = 1.24.

Distribution and ecology. Saint Helena; fallen branches of deciduous trees. So far known from two localities.

Remarks. The spines of *Protodontia insularis* are minute and thus detectable under a lens only. Two other *Protodontia* species have a more pronounced hydnoid

hymenophore and their basidiospores are of different size. *Ofella glaira* is microscopically similar to *P. insularis* but its hymenophore is completely smooth.

Protodontia subgelatinosa (P. Karst.) Pilát, Sborn. Národ. Mus. Praze 13B (4): 200, 1957. – Figs. 5d, 6i

≡ *Hydnum subgelatinosum* P. Karst., Medd. Soc. Fauna Fl. Fennica 9: 50, 1882. Lectotype. Finland. Etelä-Häme: Tammela, Mustiala, *Betula*, 2.X.1867 *Karsten 1720* (H) (selected by Reid 1990: 104).

= *Protohydnum lividum* Bres., Ann. Mycol. 1: 117, 1903. Lectotype. Poland. Podlasie, *Betula*, VI.1901 *Eichler 67* (S F21212, studied) (selected by Reid 1990: 104).

= *Protodontia uda* Höhn., Sitz. Kaiserl. Akad. Wiss. Math.-naturwiss. Klasse Abt. I 116: 83, 1907.

Basidiocarps semitranslucent, effused, gelatinous, whitish or greyish, adnate; hymenophore hydnoid, spines more or less regularly regularly arranged, sometimes fusing in groups of 3–4, acute, 0.02–0.2 mm long, 4–7 per mm; subiculum watery greyish, 0.02–0.05 mm thick, almost invisible in dry condition; margin indistinct; mineral inclusions absent.

Hyphal structure monomitic; hyphae clamped, more or less uniform, thin- or only slightly thick-walled, in spines subparallel, 2–4 µm in diam. Cystidia absent; hyphidia abundant, simple to branched, 1–3 µm in diam. at the apical part. Basidia 4-celled, (8.2–) 8.4–11.2 (–11.8) × (7.3–) 7.4–10.5 (–11.2) µm (n = 40/4), openly arranged; enucleate stalk up to 14 × 4 µm; sterigmata up to 10 × 2.5–3 µm. Basidiospores ellipsoid to ovoid, rarely cylindrical, (5.2–) 5.4–9.2 (–9.7) × (4.0–) 4.1–6.0 (–6.2) µm (n = 230/8), L = 6.25–7.66, W = 4.38–5.24, Q = 1.34–1.58.

Distribution and ecology. Europe (Denmark, Finland, France, Germany, Norway, Poland), East Asia (Russian Far East), North America (USA – California); rotten wood of deciduous trees (except one record on *Abies* in East Asia).

Remarks. *Protodontia subgelatinosa* is a widespread albeit rarely collected species. It possesses the largest basidiospores of the genus as circumscribed here.

Key to European *Myxarium* and similar-looking species

1. Basidiocarps cerebriform or adpressed-orbicular, at least 1 mm in diam., mean spore length more than 10 µm

…….……...…… 2

(1). Basidiocarps resupinate, if pustular then less than 0.5 mm in diam.

…….. 5

2. Basidiocarps adpressed-orbicular, with mineral inclusions easily visible with the naked eye … *M. nucleatum*

(2). Mineral inclusions absent or only occasionally visible

…...……...……..... 3

3. Basidiospores 9–14 × 3–5 µm, mean spore width less than 4 µm. On Salicaceae, almost exclusively on *Populus tremula*

……..…… *M. populinum*

(3). Basidiospores larger, mean spore width more than 4 µm. On various hosts

…… 4

4. Exclusively on still attached or just fallen twigs, often in bark ruptures. Basidiocarps first hyaline with light yellowish tints, then white, opaque. Northern species

…….. *M. cinnamomescens*

(4). On branches and fallen logs. Basidiocarps first ochraceous to brownish, then whitish-hyaline and containing detectable mineral inclusions (coalescent basidiocarps only). Southern species ….. *M. hyalinum*

5. Large (exceeding 60 µm long), tubular, deeply rooting cystidia present …… 6

(5). Cystidia absent or (if present) less than 50 µm long, of subhymenial origin ……..…….. 8

6. Cystidia distinctly thick-walled ……

Heterochaetella dubia s.l.

(6). Cystidia thin-walled

……. 7

7. Basidia 7–8.5 × 6–7.5 µm, basidiospores 3.5–6 × 3–5 µm. Widespread species …

Mycostilla vermiformis

(7). Basidia 9.5–11.5 × 8–11.5 µm, basidiospores 5–7 × 4–6 µm. Northern species …..

Stypellopsis hyperborea

8. Hymenophore at least in some parts hydnoid, with well-developed spines ……. 9

(8). Spine-like projections absent or occasional

..……..…… 13

9. Tramal hyphae distinctly thick-walled, cyanophilous, partly encrusted; spines 1–3 mm long, greyish ……

Hyalodon piceicola

(9). Tramal hyphae thin-walled, not encrusted; spines shorter than 1 mm ……..... 10

10. On deciduous trees

…… 11

(10). On conifers

…… 12

11. Basidiospores ellipsoid-ovoid, 5.5–9 × 4–6 µm ……. *Protodontia subgelatinosa*

(11). Basidiospores cylindrical to narrowly ellipsoid, 4–6 × 2.5–4 µm ……..…… *Myxarium legonii*

12. Spines regularly distributed on hymenial surface, basidiospores broadly ellipsoid to subglobose, 5–7 × 4–6 µm

……. *Protoacia delicata*

(12). Spines irregularly arranged, basidiospores ellipsoid-ovoid, 5.5–7 × 4–6 µm

……..……. *Gelacantha pura*

13. Basidiocarps pustular or lenticular, partly fusing to compound reticulate fructifications but remaining discernible

…… 14

(13). Basidiocarps effused, continuous

……..…… 16

14. Basidiocarps with tuft-like projections, basidia mostly 2-spored, basidiospores broadly ellipsoid to ellipsoid, 5–8.5 × 4–6 µm

…….. *Myxarium crystallinum*

(14). Tuft-like projections absent, basidia normally 4-spored, basidiospores cylindrical to ellipsoid …..… 15

15. Basidiospores 5–8 × 3–4 µm …… *Myxarium minutissimum*

(15). Basidiospores 5.5–9.5 × 3.5–5 µm ……..……. *Myxarium grilletii*

16. Basidiospores broadly ellipsoid to subglobose ……. 17

(16). Basidiospores cylindrical to narrowly ellipsoid ……. 18

17. On deciduous trees. Basidiospores 4–6 × 3.5–5 µm …..…… *Hydrophana sphaerospora*

(17). On conifers. Basidiospores 5–8 × 4–5.5 µm ……..……. *Ofella glaira*

18. Mean spore length exceeding 10 µm …….. 19

(18). Mean spore length less than 10 µm …… 20

19. Basidiocarps smooth or slightly tuberculate, margin adnate, detectable mineral inclusions absent …….. *Myxarium mesomorphum*

(19). Basidiocarps strongly tuberculate, with mineral inclusions, margin at least partly detaching ……..…. *Myxarium hyalinum* (old coalescent basidiocarps)

20. Subiculum distinct, white, consisting of thick-walled, cyanophilous hyphae …….. *Myxarium crozalcii*

(20). Subicular layer indistinct

…….. 21

21. Subhymenial hyphae interwoven, tapering hymenial cystidia present, old basidiocarps with abundant, easily visible mineral inclusions

…….. *Myxarium podlachicum*

(21). Subhymenial hyphae ascending, cystidia and detectable mineral inclusions absent

…….. 22

22. Basidia devoid of enucleate stalk, basidiospores 5–8 × 2.5–4.5 µm ……..... *Myxarium fugacissimum*

(22). Basidia pedunculate

…… 23

23. Occasional spine-like projections present on hymenial surface. Basidiospores 5–7 × 3–4 µm ……..…….. *Myxarium evanidum*

(23). Hymenial surface smooth or tuberculate. Basidiospores larger

……..…. 24

24. Basidiospores 6–10 × 3–4.5 µm, mean width less than 4 µm …… *Myxarium varium*

(24). Basidiospores 5.5–9.5 × 3.5–5 µm, mean width exceeding 4 µm

…….. *Myxarium grilletii* (old coalescent basidiocarps)

Discussion

Our study shows that sphaeropedunculate basidia occur in several, distantly related lineages of the *Auriculariales* and that it is an important character at the generic level.

This outcome agrees with earlier results of Weiss and Oberwinkler (2001). The only exceptional case so far detected is *M. fugacissimum* with non-stipitate basidia; an absence of enucleate stalk in the latter species may be connected with the extreme thinness of its basidiocarps. Sphaeropedunculate basidia have been found in other genera of the order having more complex, pileate, stipitate and even clavarioid fructifications (*Pseudohydnum*, *Tremiscus*, *Tremellodendropsis* s. lato) or poroid basidiocarps (*Protomerulius*). Further studies with larger taxon sampling and additional genes can provide better evidence concerning the taxonomic value of this morphological feature.

The generic splitting proposed in the present paper followed a balanced approach. In particular, the genus *Myxarium* is accepted in the broadest possible sense, i.e. including the distantly related *M. crystallinum*, mainly due to high morphological similarity of it with other *Myxarium* spp. However, we cannot preclude that using other genetic markers will necessitate a separate genus for *M. crystallinum*. The opposite example is a group of the monotypic genera *Tremiscus*, *Gelacantha* and *Protoacia*. In ITS + LSU phylogeny, they were uncovered in one clade although without statistical support. The representatives of these genera show extremely similar microscopic traits but they have clearly different macroscopic habit, host preferences and geographic distribution (although too little information is so far available about distribution and ecology of *G. pura*). Considering our current knowledge of these taxa, we found it unavoidable to introduce two new genera, *Gelacantha* and *Protoacia*, for two newly described species, *G. pura* and *P. delicata*. Nevertheless, sampling myxarioid fungi outside Europe and sequencing non-ribosomal genes may facilitate better generic delimitation in this complex.

In total, 23 species from seven genera have been included in the present paper. Morphologically, they are rather simply constructed, producing effused basidiocarps (except two exidioid species) with smooth, tuberculate or spiny hymenophore. Hyphae are poorly differentiated between subiculum and subhymenium, and most taxa are devoid of cystidia. Morphology-based species identification is possible, at least in Europe, if host tree species, basidiocarp configuration and dimensions of basidia and basidiospores are considered. For microscopic investigation, the combination of Cotton Blue as a mountant and phase contrast illumination is strongly recommended.

The variability of ITS sequences in *M. fugacissimum – M. podlachicum* and *M. mesomorphum – M. nucleatum* complexes deserves a closer look. It is possible that more material from different geographic regions and non-ribosomal gene sequences will disclose much larger species diversity than dealt with above. The intercontinental differences in ITS sequences of *M. grilletii* and *M. legonii* also may indicate that they are collective species. We were unable to verify this hypothesis due to the sparsity of recent collections.

Morphological examination of two tropical taxa, *Sebacina gleophilum* L.S. Olive (Tahiti, holotype, NY) and *Tremella inconspicua* Pat. (Ecuador, holotype, FH), indicates they belong to this group of species, but no recent material has been available for sequencing. However, a short collecting trip in Africa (by the author AS) revealed five new species of *Myxarium* and *Protodontia*, as detailed above. This is a good indication of a high diversity of the studied group in tropical areas.

Specimens examined (sequenced collections are marked by asterisk)

Exidia alboglobosa. France. Vienne: Savigné, *Robinia pseudoacacia* (?), 23.XI.1924 *Grelet* (BPI 701610, lectotype).

Gelacantha pura. Russia. Karachaevo-Cherkessia: Karachaevsk Dist, Teberda Nat. Res., *Abies obovata*, 19.VIII.2009 *Malysheva* (LE 254018*, holotype).

Hyalodon piceicola. Estonia. Jõgevamaa: Rebase, Puurmani, rotten stems of *Athyrium filix-femina*, 1.X.1957 Parmasto (TAAM 006683, holotype of *Protodontia filicina*).

Hydrophana sphaerospora. Denmark. Hovedstaden: Lyngby-Taarbæk, Ørholm, wood, 9.X.1982 *Hauerslev 6197* (C, lectotype of *Myxarium leptocystidiatum*). France. Aveyron: Loubotis, *Alnus glutinosa*, 9.IX.1914 *Galzin 16069* (K, PC, lectotype and isolectotype of *Sebacina sphaerospora*). Norway. Vest-Agder: Mandal, Uføra, *Quercus robur*, 2.XI.2017 *Spirin 11779* (O). Aust-Agder: Grimstad, Sæveli, *Q. robur*, 2.XI.2017 *Spirin 11786, 11790* (O). Oppland: Lunner, Rinilhaugen, *Sorbus aucuparia*, 17.IX.2016 *Spirin 11133*, 11142* (O). Møre og Romsdal: Nesset, Eikesdalen, hardwood, 27.IX.2017 *Spirin 11606* (O), *Alnus incana*, 28.IX.2017 *Spirin 11622** (O).

Myxariellum concinnum. USA. Washington: Pend Oreille Co., Sullivan Creek, *Thuja plicata*, 13.X.2014 *Spirin 8393c** (H, holotype).

Myxariellum tenerum. USA. Washington: Pend Oreille Co., Gypsy Meadows, *Picea engelmannii*, 17.X.2014 *Spirin 8685** (H, holotype).

Myxarium cinnamomescens. Estonia. Viljandimaa: Lemmjõe, *Tilia cordata*, 17.IX.2018 *Spirin 12349* (H, TU). Norway. Akershus: Nannestad, Nannestad, *Alnus* sp., 19.IX.1990 *Torkelsen 324/90* (O F295316). Russia. Leningrad Reg.: Boksitogorsk Dist., Chagoda, *Populus tremula*, 21.VIII.2018 *Spirin 12216* (H). Nizhny Novgorod Reg.: Lukoyanov Dist., Panzelka, *Tilia cordata*, 2.VIII.2017 *Spirin 11317** (H, LE), Razino, *T. cordata*, 3.VIII.2017 *Spirin 11350** (H, LE), *T. cordata*, 4.VIII.2017 *Spirin 11373* (H), Sanki, *T.*

cordata, 4.VIII.2017 *Spirin 11372* (H); Pavlovo Dist., Vorsma, *T. cordata*, 6.VIII.2017 *Spirin 11381* (H, LE). For other specimens examined, see Spirin et al. 2017.

Myxarium cirratulum. Kenya. Taita-Taveta: Taita Hills, Chawia, hardwood branch, 26.XI.2017 *Savchenko 171126/1117** (H, holotype, EA).

Myxarium crozalcii. Armenia. Tavush: Noyemberyan, hardwood, 14.IX.1962 *Raitviir* (TAAM 043018a). Canada. Ontario: Brant Co., New Durham, *Ulmus* sp., 30.VIII.1937 *Cain* (TRTC 17594, holotype of *Heterochaetella bispora*). France. Aveyron: St. Sernin, Frégère, *Cerasus* sp., 21.XII.1909 *Galzin 5168* (PC, lectotype of *Sebacina opalea* f. *stratosa*); without exact locality, *Malus* sp., 9.IV.1910 *Galzin 5450* (herb. Bourdot 8341) (PC 0706757). Var: Toulon, *Quercus* sp., 2.XII.1925 *Crozalc 23*, 17.IV.1925 *Crozalc 38* (PC, syntypes of *Sebacina crozalcii*). Germany. Sachsen-Anhalt: Halberstadt, Schwanebeck, *Betula* sp., 3.X.1994 *Hechler 94.235* (HBG). Norway. Telemark: Porsgrunn, Mule Varde, hardwood, 10.X.2013 *Molia 247* (O F21913). Russia. Khabarovsk Reg.: Khabarovsk Dist., Ulun, *Syringa amurensis*, 26.VIII.2012 *Spirin 5630** (H). Nizhny Novgorod Reg.: Lukoyanov Dist., Razino, *Tilia cordata*, 16.VIII.2015 *Spirin 9317, 9334* (H), 10.VIII.2016 *Spirin 10629* (H), 3.VIII.2017 *Spirin 11334** (H), 25.VIII.2018 *Spirin 12043* (H). Sakha Rep.: Yakutsk Dist., Spasskaya Pad, *Betula platyphylla*, 5.VIII.1999 *Kotiranta 15827* (H), Borisovka, *B. platyphylla*, 14.VIII.1999 *Kotiranta 16143* (H). Spain. Barcelona, Cabrils, 31.X.1979 *Tellería 164/79* (MA F62053). Ukraine. Luhansk Reg.: Stanichno-Luhansky Dist., Luhansk Nat. Res., *Betula pendula*, 20.X.2010 *Ordynets* (CWU 4197*). USA. Iowa: Dubuque Co., White Pine Hollow, hardwood, 22.VI.1940 *Martin* (TAAM 193053).

Myxarium crystallinum. Denmark. Hovedstaden: Dragør, Kongelunden, wood, 12.X.1980 *Hauerslev 5920* (C, holotype of *Stypella parvula*); Lyngby-Taarbæk, Ørholm, wood, 19.XI.1976 *Hauerslev 5264* (C, holotype of *Myxarium gilvum*).

Norway. Møre og Romsdal: Nesset, Eikesdalen, *Ulmus glabra*, 27.IX.2017 *Spirin 11597* (O), hardwood, 27.IX.2017 *Larsson 17542** (O). United Kingdom. England, Surrey, Ockley, Vann Lake, rotten stump, 22.X.1972 *Reid & Petch* (K, holotype).

Myxarium evanidum. Norway. Akershus: Asker, Esvika, decayed wood, 30.IX.2017 *Larsson 17638, 17642** (O). Møre og Romsdal: Nesset, Eikesdalen, *U. glabra*, 28.IX.2017 *Spirin 11615** (O, holotype).

Myxarium frumentaceum. Kenya. Taita-Taveta: Taita Hills, Chawia forest, hardwood branch, 26.XI.2017 *Savchenko 171126/1400** (H, holotype, EA), Mbololo forest, hardwood branches, 29.XI.2017 *Savchenko 171129/1350** (H, EA), *171129/1450B** (H, EA).

Myxarium fugacissimum. Estonia. Tartumaa: Elva, Mälgi, *A. incana*, 20.IX.2018 *Spirin 12388* (H, TU). France. Aveyron: St. Estève, *Quercus* sp., 5.V.1915 *Galzin 17914* (PC, lectotype of *Sebacina fugacissima*); without exact locality, *F. excelsior* and rotten basidiocarps of *Inonotus hispidus*, 3.III.1910 *Galzin 4395* (herb. Bourdot 20080) (PC 0706762), *F. excelsior*, no date, *Galzin 24513* (herb. Bourdot 26541) (PC 0706761). Norway. Buskerud: Rien, Stokkerinden, *U. glabra*, 29.IX.2018 *Spirin 12486* (O). Russia. Karachaevo-Cherkessia: Karachaevsk Dist., Teberda Nat. Res., *Fagus sylvatica*, 6.VIII.2009 *Malysheva* (LE 253858*). Nizhny Novgorod: Pavlovo Dist., Chudinovo, *T. cordata*, 10.IX.2018 *Spirin 12309* (H). Primorie: Khasan Dist., Land of the Leopard Nat. Park, *Quercus* sp., 2.IX.2011 *Malysheva* (LE 262916*); Shkotovo Dist., Ussurisky Nat. Res., decayed wood, 15.VIII.2011 *Malysheva* (LE 262940).

Myxarium grilletii. Armenia. Syunik: Tsav, *Juglans regia*, 2.X.1962 *Raitviir* (TAAM 043111). Canada. Alberta: Edmonton, Henrietta Louise Edwards Park, *Populus alba*, 28.VII.2015 *Spirin 9016** (H). Norway. Oppland: Nord-Fron, Liadalane Nat. Res., *U. glabra*, 12.IX.2016 *Spirin 11047** (O), *P. tremula*, 29.IX.2017 *Spirin 11653** (O). USA.

Massachusetts: Norfolk Co., Canton, *Malus* sp., 19.IV.1934 *Linder* (Reliquiae Farlowianae #787, H ex FH).

Myxarium hyalinum. France. Hérault: Fournouls, *Quercus ilex*, 22.X.1979 *Torkelsen 408/79* (O), St. Amans de Mounis, *Fagus sylvatica*, 21.X.1979 *Torkelsen 379/79* (O). Germany. Schleswig-Holstein: Ostholstein, Malente, *T. cordata* (?), 3.X.2000 *Hechler A0.042* (HBG). Norway. Vest-Agder: Mandal, Uføra, *T. cordata*, 2.XI.2017 *Spirin 11778** (O). For other specimens examined, see Spirin et al. 2017.

Myxarium legonii. Canada. Alberta: Edmonton, Louise McKinney Riverfront Park, *P. alba*, 28.VII.2015 *Spirin 8986** (H). Malawi. Southern Prov.: Thyolo, Naminkweya estate, rotten wood, 3–4.III.1973 *Ryvarden 11205* (O). Russia. Nizhny Novgorod Reg.: Lukoyanov Dist., Razino, *U. glabra*, 18.VIII.2015 *Spirin 9511** (H). United Kingdom. England: Surrey, Runnymede, Cooper's Hill, *Ulmus* sp., 5.III.1988 *Legon* (K, holotype), *Ulmus* sp., 31.VI.1988 *Legon* (TAAM 132119). USA. New York: Essex Co., Arbutus Lake, decayed wood, 17.VIII.2012 *Miettinen 15677** (H). Tennessee: Sevier Co., Ramsey Cascades Trail, decayed wood, 13.VII.2004 *Larsson 12177* (GB, H).

Myxarium mesomorphum. Finland. Etelä-Häme: Tammela, Mustiala, *Syringa vulgaris*, 16.X.1888 *Karsten 4942* (H). France. Aveyron: Boutaran, *Rosa canina*, 12.V.1914 *Galzin 15287* (PC, lectotype of *Sebacina mesomorpha*). Norway. Vest-Agder: Mandal, Uføra, *P. tremula*, 2.XI.2017 *Spirin 11782* (O). Akershus: Asker, Esvika, *T. cordata*, 28.IX.2018 *Spirin 12474* (O). Oslo: Oslo, Hovedøya, *T. cordata*, 10.IV.1980 *Ligaard* (O F295123). Møre og Romsdal: Nesset, Eikesdalen, *Sorbus* sp., 27.IX.2017 *Spirin 11613** (O). Nordland: Saltdal, Junkerdalsura, *Betula* sp., 27.VIII.1988 *Torkelsen 199b/88* (O F295419). Russia. Leningrad Reg.: Podporozhie Dist., Grishino, *T. cordata*, 16.IX.2017 *Spirin 11383** (H).

Myxarium minutissimum. France. Aveyron: Bordes, *A. glutinosa*, 24.VIII.1915 *Galzin 18440* (herb. Bourdot 19816) (PC 0084239). France. Gironde: Bordeaux, *Populus*, X.1915 *Galzin 18518* (K(M) 48787, lectotype of *Tremella glacialis*). Moselle: Moyeuvre-Petit, decayed wood, 11.IX.2003 *Trichies 03081* (H, GT). Rhône: St. Germain au Mont d'Or, *Quercus petraea*, 25.X.2013 *Van Vooren* (LY-BR 5270, holotype of *Myxarium grilletii* f. *invisibile*). Norway. Vest-Agder: Lyngdal, Fladstad, *Q. robur*, 1.XI.2017 *Spirin 11757* (O). Vestfold: Larvik, Jordstøyp i Kvelde, *Acer platanoides*, 15.IX.2016 *Spirin 11100, 11103** (O). Oppland: Sør-Fron, Lågen, rotten wood, 14.V.1989 *Torkelsen 120/89* (O F295156). Møre og Romsdal: Nesset, Eikesdalen, *U. glabra*, 28.IX.2017 *Spirin 11623** (O). Russia. Leningrad Reg.: Tikhvin Dist., Korbenichi, *Salix caprea*, 22.VIII.2018 *Spirin 12240* (H).

Myxarium nucleatum. Austria. Niederösterreich: Pulkau, Groß-Reipersdorf, *Vitis vinifera*, 7.VII.1986 *Hausknecht* (dupl. *Hechler 86.049*, HBG). Germany. Bayern: Bayreuth, Freienfels, *T. cordata*, 20.II.1990 *Engel 12632* (*Hechler 90.014*) (HBG). Niedersachsen: Lüchow-Dannenberg, *T. cordata* (?), 1.X.1996 *Hechler 96.105* (HBG). Norway. Vest-Agder: Skoland, *T. cordata*, 1.XI.2017 *Spirin 11768** (O). Russia. Nizhny Novgorod Reg.: Lukoyanov Dist., Razino, *T. cordata*, 3.VIII.2017 *Spirin 11336* (H), Sanki, *T. cordata*, 4.VIII.2017 *Spirin 11371* (H). For other specimens examined, see Spirin et al. 2017.

Myxarium aff. *nucleatum.* Norway. Vest-Agder: Lyngdal, Fladstad, *Ilex aquifolium*, 1.XI.2017 *Spirin 11760** (O).

Myxarium podlachicum. Canada. Alberta: Edmonton, Louise McKinney Riverfront Park, *P. alba*, 28.VII.2015 *Spirin 8984** (H). Ontario: Nipissing Dist., Temagami, on wood, 3.VIII.1937 *Luck-Allen* (H ex TRTC 31562). Estonia. Viljandimaa: Pääsma, *T. cordata*, 18.IX.2018 *Spirin 12377* (H, TU). Finland. Etelä-Häme: Hämeenlinna, Lammi,

Betula pubescens, 15.IX.2015 *Miettinen 19338** (H). Germany. Niedersachsen: Lüchow-Dannenberg, *Betula* sp. and dead basidiocarps of *Fomes fomentarius*, 22.IX.1994 *Hechler 94.177* (HBG). Norway. Vestfold: Larvik, Jordstøyp i Kvelde, *P. tremula*, 15.IX.2016 *Spirin 11105** (O). Telemark: Bamble, Rognsheia, *Ulmus* sp., 3.XI.2017 *Spirin 11795** (O), *Corylus avellana*, 3.XI.2017 *Spirin 11794, 11805* (O), *11815* (infected by *Achroomyces insignis*) (O); Nome, Mörkvasslia Nat. Res., *A. incana*, 25.X.2016 *Spirin 11201* (infected by *A. insignis*), *11203** (O). Akershus: Asker, Esvika, *C. avellana*, 30.IX.2017 *Spirin 11670** (O), *Ulmus* sp., 30.IX.2017 *Spirin 11680* (infected by *A. insignis*) (O). Hedmark: Stange, Rotlia, *C. avellana*, 26.IX.2018 *Spirin 12419, 12427* (both infected by *A. insignis*). Oppland: Nord-Fron, Liadalane Nat. Res., *A. incana*, 29.IX.2017 *Spirin 11646*, 11650* (O). Møre og Romsdal: Nesset, Eikesdalen, *U. glabra*, 28.IX.2017 *Spirin 11616** (O). Poland. Mazovia (lectotype of *Sebacina podlachica*, see below). Russia. Leningrad Reg.: Podporozhie Dist., Vazhinka, *B. pubescens*, 17.IX.2017 *Spirin 11510** (H). Nizhny Novgorod Reg.: Bogorodsk Dist., Krastelikha, *Q. robur*, 2.X.2015 *Spirin 9857, 9908** (H). United Kingdom. England, East Sussex, Buckhurst Wood, *Fagus sylvatica*, 30.X.1926 *Pearson* (K, lectotype of *Sebacina subhyalina*).

Myxarium populinum. Estonia. Viljandimaa: Tipu, Kikepera, *P. tremula*, 16.IX.2018 *Spirin 12340* (H, TU). Norway. Aust-Agder: Risør, Glupedalen, *P. tremula*, 26.VIII.2000 *Dahl 113/2000* (O F295422). Troms: Storfjord, Skibotndalen, *P. tremula*, 19.VIII.1992 *Torkelsen 95/92* (O F295526). Russia. Leningrad Reg.: Boksitogorsk Dist., Chagoda, *P. tremula*, 21.VIII.2018 *Spirin 12208* (H); Podporozhie Dist., Oksozero, *P. tremula*, 16.IX.2017 *Spirin 11448* (H, LE). Nizhny Novgorod Reg.: Lukoyanov Dist., Panzelka, *P. tremula*, 2.VIII.2017 *Spirin 11314** (H, LE). For other specimens examined, see Spirin et al. 2017.

Myxarium rotundum. Kenya. Taita-Taveta: Taita Hills, Chawia, hardwood branch, 27.XI.2017 *Savchenko 171127/1025** (H, holotype, EA).

Myxarium simile. Kenya. Taita-Taveta: Taita Hills, Mbololo forest, hardwood branch, 29.XI.2017 *Savchenko 171129/1120A** (H, holotype, EA).

Myxarium varium. Denmark. Sjælland: Faxe, Vemmetofte Skov, wood, 23.IX.1977 *Hauerslev 6097* (C, holotype). Estonia. Viljandimaa: Pääsma, *U. glabra*, 18.IX.2018 *Spirin 12358* (H, TU). Finland. Etelä-Häme: Pirkkala, Pakkalankulma, *Salix* (?), 15.IX.2014 *Söderholm 4778* (H) (infected by *Achroomyces subabditus*). France. Meurthe-et-Moselle: Sancy, Les Fontaines de Corbey, fallen decorticated branch (deciduous tree), 11.XI.2008 *Trichies 08379* (GT, H). Moselle: Havange, decorticated branch (*Populus nigra* or *Alnus glutinosa*), 12.VI.1999 *Trichies 99199* (GT, H), *A. glutinosa*, 22.II.2001 *Trichies 01040* (GT, H). Germany. Hamburg: Harburg, Neugraben, *Quercus* sp., 27.VIII.1992 *Hechler 92.060* (HBG), 13.III.1995 *Hechler 95.007* (HBG). Sachsen-Anhalt: Sangerhausen, Grillenberg, *F. sylvatica*, 2.IX.1995 *Hechler 95.096* (HBG). Norway. Akershus: Asker, Stokkerelva at Åstaddammen, *U. glabra*, 28.IX.2018 *Spirin 12442* (O). Buskerud: Rien, Stokkerinden, *A. incana*, 29.IX.2018 *Spirin 12487* (O). Møre og Romsdal: Nesset, Eikesdalen, *A. incana*, 27.IX.2017 *Spirin 11600** (O); Sunndal, Sogge bru, *A. incana*, 20.VIII.1991 *Torkelsen 307/91* (O F160475). Russia. Nizhny Novgorod Reg.: Lukoyanov Dist., Panzelka, *B. pubescens*, 2.VIII.2017 *Spirin 11323** (H, LE), Razino, *U. glabra*, 24.VII.2018 *Spirin 12008* (H). Sweden. Dalsland: Edsleskog, *C. avellana*, 12.IX.1990 *Laessøe* (O F160476).

Ofella glaira. Estonia. Pärnumaa: Häädemeeste, Pärnu parish, *Pinus sylvestris*, 7.VIII.1960 *Raitviir* (TAAM 040840). Finland. Uusimaa: Helsinki, Toukola, conifer (?), 3.X.2007 *Miettinen 11963.1* (H). Norway. Telemark: Bamble, Rognsheia, *Picea*

abies, 3.XI.2017 *Spirin 11809** (O). Sweden. Småland (lectotype of *Tremella glaira*, see below).

Protoacia delicata. Norway. Akershus: Nannestad, Tømte, *P. abies*, 18.IX.1990 *Ryvarden 28777* (O F179612). Hedmark: Trysil, Smoldalen, *P. abies*, 9.IX.2004 *Ryvarden 46664* (O F179171). Møre og Romsdal: Aure, Lovika, *P. sylvestris*, 10.IX.2003 *Oldervik 453.03* (O F189376). Sør-Trøndelag: Selbu, Råndalen, *P. abies*, 20.IX.2011 *Nordén 9326* (O F248082); Tydal, *P. abies*, 3.XI.2011 *Nordén 9568** (O). Nord-Trøndelag: Levanger, Forra, *P. abies*, 25.IX.1972 *Siversten* (O F87779). Nordland: Rana, Ravnå, *P. abies*, 9.IX.1976 *Ryvarden* (O F87783); Saltdal, Evenesdalen, *P. abies*, 29.VIII.1988 *Ryvarden 25501* (O F87782). Russia. Khabarovsk Reg.: Khabarovsk Dist., Bolshoi Khekhtsir, *P. ajanensis*, 4.IX.2013 *Spirin 6637* (H); Verkhnebureinskii Dist., Hegdy, *Picea ajanensis*, 22.VIII.2014 *Spirin 7824** (H), Dublikan Nat. Res., *P. ajanensis*, 23.VIII.2014 *Spirin 7947* (H). Leningrad Reg.: Boksitogorsk Dist., Chagoda, *P. abies*, 24.IX.2011 *Spirin 4615** (H, holotype). Sweden. Jämtland: Krokom, *P. abies*, 14.IX.2011 *Svantesson 324* (O).

Protodontia africana. Kenya. Taita-Taveta: Taita Hills, Chawia, hardwood branch, 26.XI.2017 *Savchenko 171126/1104** (H, holotype, EA).

Protodontia insularis. St. Helena. Diana Peak Nat. Park, hardwood, 2.II.2014 *Ryvarden 49417** (H – holotype, K – isotype), *49418* (K); Thomson's Wood, hardwood, 6.II.2014 *Ryvarden 49594* (K).

Protodontia subgelatinosa. Finland. Varsinais-Suomi: Parainen, Seili, *A. glutinosa*, 26.V.2011 *Miettinen 14445* (H). Uusimaa: Helsinki, Veräjämäki, *A. incana*, 5.IX.2011 *Miettinen 14682.3* (H), *A. incana* or *S. caprea*, 21.X.2011 *Miettinen 14934.1** (H). Etelä-Häme: Nokia, Pinsiö, *B. pubescens*, 17.X.2004 *Söderholm 3575* (H). Pohjois-Häme: Jyväskylä, Vuoritsalo, *A. glutinosa*, 21.VII.2007 *Miettinen 11794* (H). France.

Moselle: Havange, *A. glutinosa*, 16.V.2003 *Trichies 03032* (GT, H). Germany. Niedersachsen: Rotenburg, Sittensen, hardwood, 14.VII.2001 *Hechler A1.014* (HBG). Norway. Vestfold: Borre, Borrenhaugene, *Betula* sp., 1.X.1989 *Marstad 110-89* (O F87777). Buskerud: Hole, Sønsterudelva, *U. glabra*, 19.X.2008 *Hofton 08949* (O F293203). Oppland: Nord-Fron, Liadalane Nat. Res., *A. incana*, 12.IX.2016 *Spirin 11038** (O), 29.IX.2017 *Spirin 11644* (O); Vågå, Veogjelet, *B. pubescens*, 13.IX.2016 *Spirin 11079** (O). Hedmark: Løten, Hørsand, hardwood, 19.IX.1987 *Høgholen 468/87* (O F87776). Nordland: Saltdalen, Evenesdalen, *A. incana*, 30.VIII.1988 *Ryvarden 25501* (O F87775). Finnmark: Kárášjohka, *B. pubescens*, 4.IX.2008 *Miettinen 13489** (H). Poland. Podlasie, *Betula*, VI.1901 *Eichler 67* (S, lectotype of *Protohydnum lividum*). Russia. Khabarovsk Reg.: Khabarovsk Dist., Birakan, *Abies nephrolepis*, 10.VIII.2012 *Spirin 5123** (H). USA. California: Napa Co., Hennessey, rotten wood, 29.XII.1960 *Wells* (TAAM 193029), Robert L. Stevenson Memorial State Park, rotten wood, 19.XII.1965 *Wells* (TAAM 193028, 193030, 193031, 193032).

Sebacina laccata. France. Aveyron: l'Hospitalet, Larzac, *Pinus* sp., 25.IV.1910 *Galzin 5743* (herb. Bourdot 7199) (PC, lectotype).

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References

Boudier, J.L.E. 1885. Description de quelques espèces nouvelles de champignons basidiosporés. – Bull. Soc. Bot. France 32: 282-285

Bourdot, H. and Galzin, A. 1924. Heterobasidiae nondum descriptae. – Bull. Soc. Mycol. France 39: 261-266

Donk, M.A. 1966. Check list of European hymenomycetous Heterobasidiae. – Persoonia 4: 145-335

Garbelotto, M. et al. 1998. The European S and F intersterility groups of *Heterobasidion annosum* may represent sympatric protospecies. – Canadian J. Bot. 76: 397-409

Gaignon, M. et al. 2015. *Myxarium grilletii* f. *invisibile* f. nov., récolté en région lyonnaise (France, Rhône). – Bull. Mens. Soc. Linn. Lyon 84: 31-37

Gardes, M. and Bruns, T.D. 1993. ITS primers with enhanced specificity for basidiomycetes – applications to the identification of mycorrhizae and rusts. – Molec. Ecol. 2: 113-118

Hauerslev, K. 1993. The genus *Myxarium* (Tremellales) in Denmark. – Mycotaxon 49: 235-256

Hopple, J. and Vilgalys, R. 1994. Phylogenetic relationships among coprinoid taxa and allies based on data from restriction site mapping of nuclear RDNA. – Mycologia 86: 96-107

Höhnel, F. 1904. Mycologische Fragmente. – Ann. Mycol. 2: 38-60

Kirschner, R. and Chen, C.J. 2004. *Helicomyxa everhartioides*, a new helicosporous sporodochial hyphomycete from Taiwan with relationships to the *Hyaloriaceae* (Auriculariales, Basidiomycota). – Stud. Mycol. 50: 337-342

Kizimova-Horovitz, L. et al. 2000. Basidiomicetos resupinados de Costa Rica. *Myxariaceae* s. Jülich, *Sebacinaceae* Wells & Oberw. y *Tremellodenropsidaceae* Jülich. – Rev. Biol. Trop. 48: 519-538

Kumar, S. et al. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. – Molec. Biol. Evol. 33: 1870-1874

Landvik, S. 1996. *Neolecta*, a fruit-body producing genus of the basal ascomycetes, as shown by SSU and LSU rDNA sequences. Mycol. Res. 100: 199-202

Malysheva, V. et al. 2018. Revision of *Protohydnum* (Auriculariales, Basidiomycota). – Mycol. Progress 17: 805-814

McLaughlin, D.J. and Spatafora, J.W. (eds.) 2014. The Mycota. VII. Systematics and Evolution. Part A. – Springer.

Rambaut, A. et al. 2014. Tracer v1.6. http://tree.bio.ed.ac.uk/software/tracer/ (accessed on 20.12.2017).

Raitviir, A. 1971. The tremellaceous fungi of the Far East. – In: Parmasto, E. (ed.). Plants and animals of the Far East. Valgus, pp. 84-148

Reid, D.A. 1970. New or interesting records of British hymenomycetes. IV. – Trans. Brit. Mycol. Soc. 55: 413-441

Reid, D.A. 1973. New or interesting records of British hymenomycetes. V. – Persoonia 7: 293-303

Reid, D.A. 1990. New or interesting records of British Heterobasidiomycetes. – Mycol. Res. 94: 94-108

Roberts, P. 1993. *Exidiopsis* species from Devon, including the new segregate genera *Ceratosebacina*, *Endoperplexa*, *Microsebacina*, and *Serendipita*. – Mycol. Res. 97: 467-478

Roberts, P. 1998. A revision of the genera *Heterochaetella*, *Myxarium*, *Protodontia*, and *Stypella* (Heterobasidiomycetes). – Mycotaxon 69: 209-248

Ronquist, F. et al. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. – Syst. Biol. 61(3): 539-542

Spirin, V. et al. 2017. On some forgotten species of *Exidia* and *Myxarium* (Auriculariales, Basidiomycota). – Nordic J. Bot. 36 (3):e01601:1-11

Spirin, V. et al. 2019. Studies in the *Stypella vermiformis* group. – Antonie van Leeuwenhoek 112: 753–764.

Tedersoo, L. et al. 2008. Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. – New Phytol. 180: 479-490

Thiers, B. 2018. Index Herbariorum: a global directory of public herbaria and associated stuff [continuosly updated]. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih

Vilgalys, R. and Hester, M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. – J. Bacteriology 172: 4238-4246

Weiss, M. and Oberwinkler, F. 2001. Phylogenetic relationships in Auriculariales and related groups – hypotheses derived from nyclear ribosomal DNA sequences. – Mycol. Res. 105: 403-415

Weiss, M. et al. 2004. Spotlights on heterobasidiomycetes. In: Agerer R. et al. (eds.) Frontiers in Basidiomycote Mycology. IHW-Verlag, pp 7-48

Wells, K. 1961. Studies of some Tremellaceae. IV. *Exidiopsis*. – Mycologia 53: 317-370

Wells, K. 1964. The basidia of *Exidia nucleata*. II. Development. – American J. Bot. 51: 360-370

Wells, K. et al. 2004. Observations on some species of *Myxarium* and reconsideration of the Auriculariaceae and Hyaloriaceae (Auriculariales). – In: Agerer R. et al. (eds) Frontiers in Basidiomycete Mycology. IHW-Verlag, pp. 237–248

White, T.J. et al. 1990. Amplification and sequencing of fungal ribosomal RNA genes for phylogenetics. – In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds.). PCR protocols. A guide to methods and applications. Academic Press, pp. 315-322

Figure Legends

Fig. 1. Combined phylogenetic nrITS+nrLSU topology from maximum likelihood analysis showing main lineages within *Auriculariales*. All sequences generated for this study are indicated in bold faces. Collection numbers of specimens are given for all sequences. Full red circle indicates clades that include taxa with sphaeropedunculate basidia (empty circle indicates absence of this feature). Support values (ML/BA) are given above the branches. Scale bar shows expected changes per site.

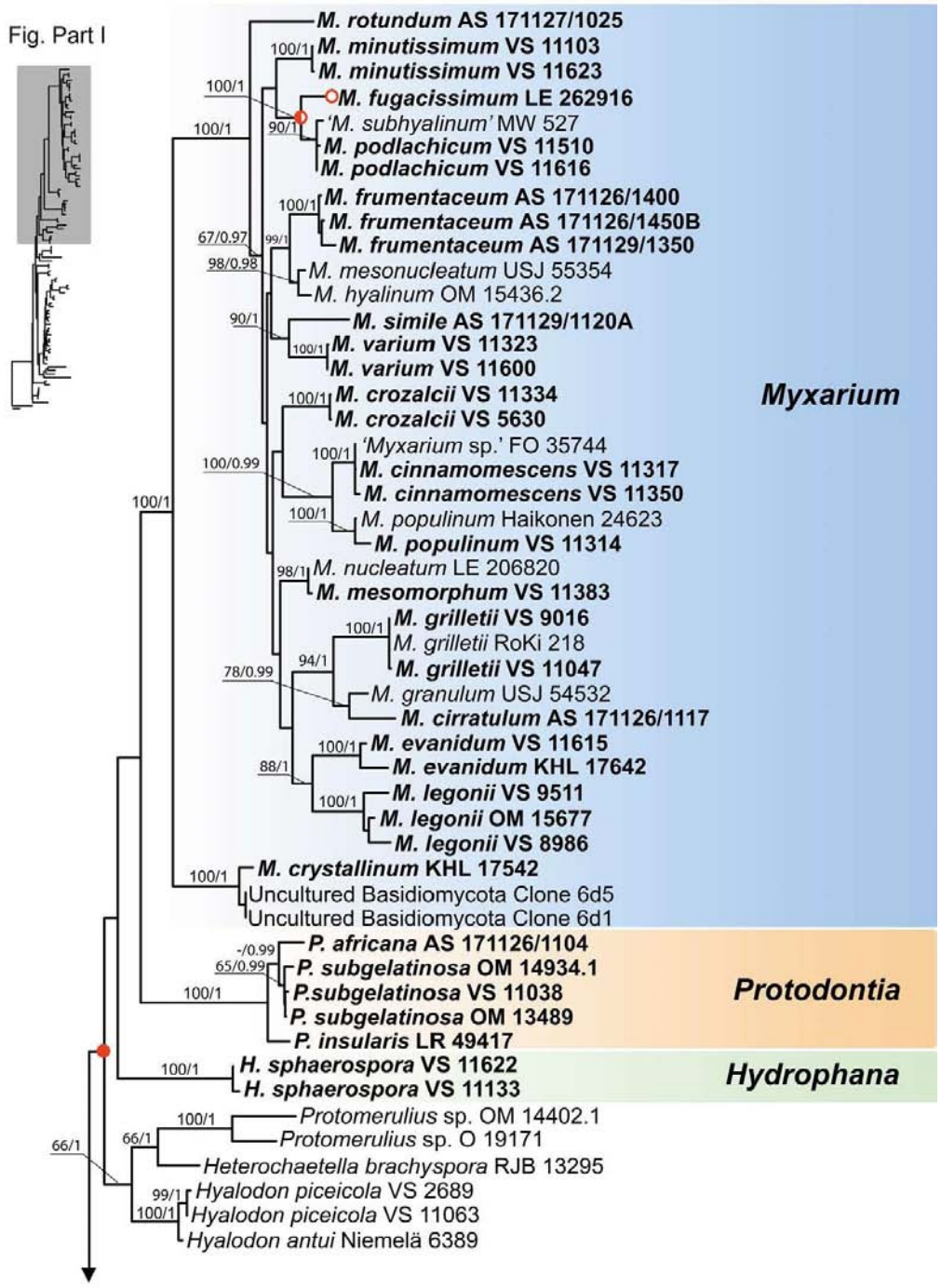

Fig. Part II

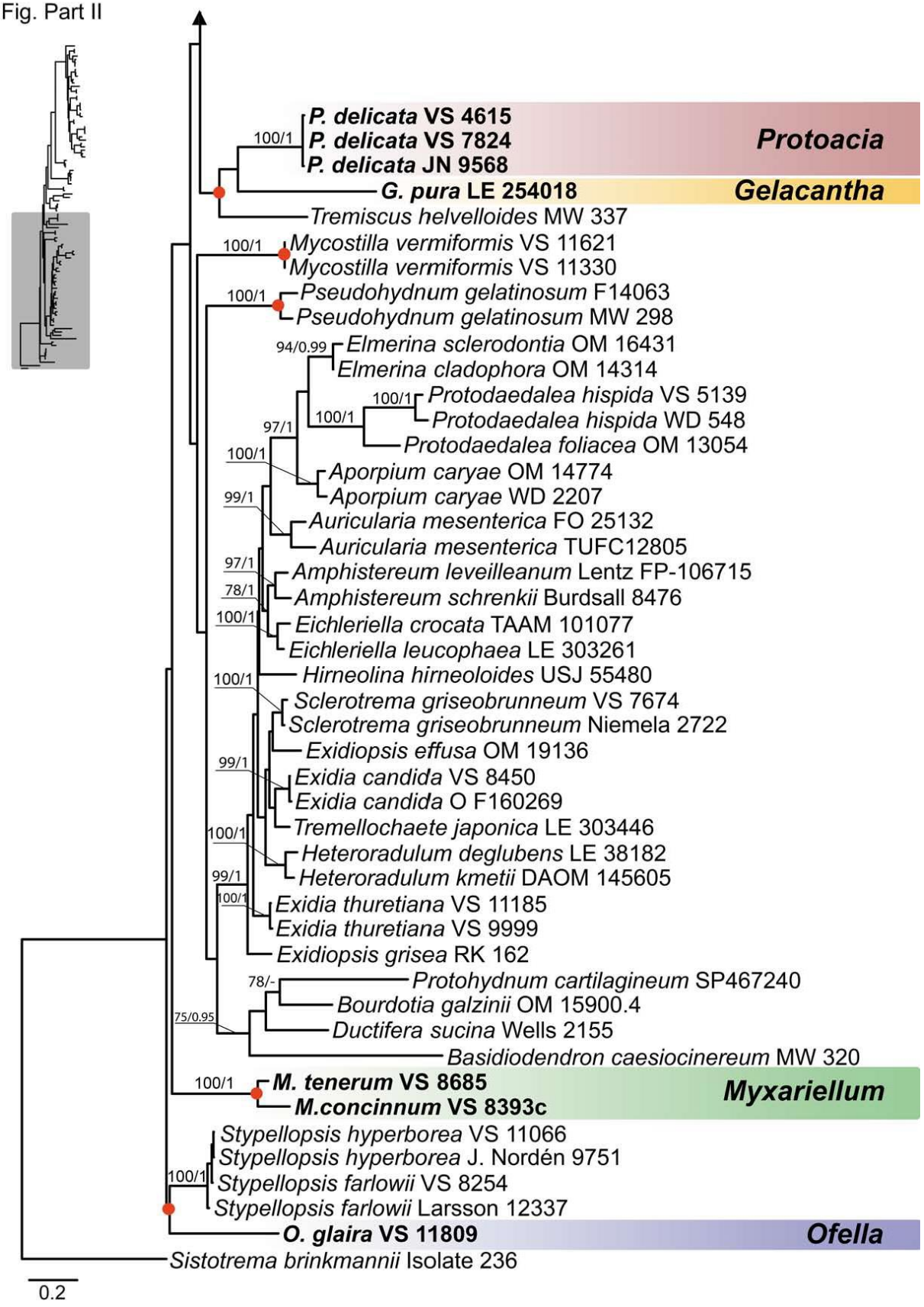

Fig. 2. Best tree from Maximum likelihood analysis for the nrITS dataset, showing phylogenetic relationships of *Myxarium* species. All sequences generated for this study are indicated in bold faces. Collection numbers of specimens are given for all sequences. Support values (ML/BA) are given on the branches. Scale bar shows expected changes per site.

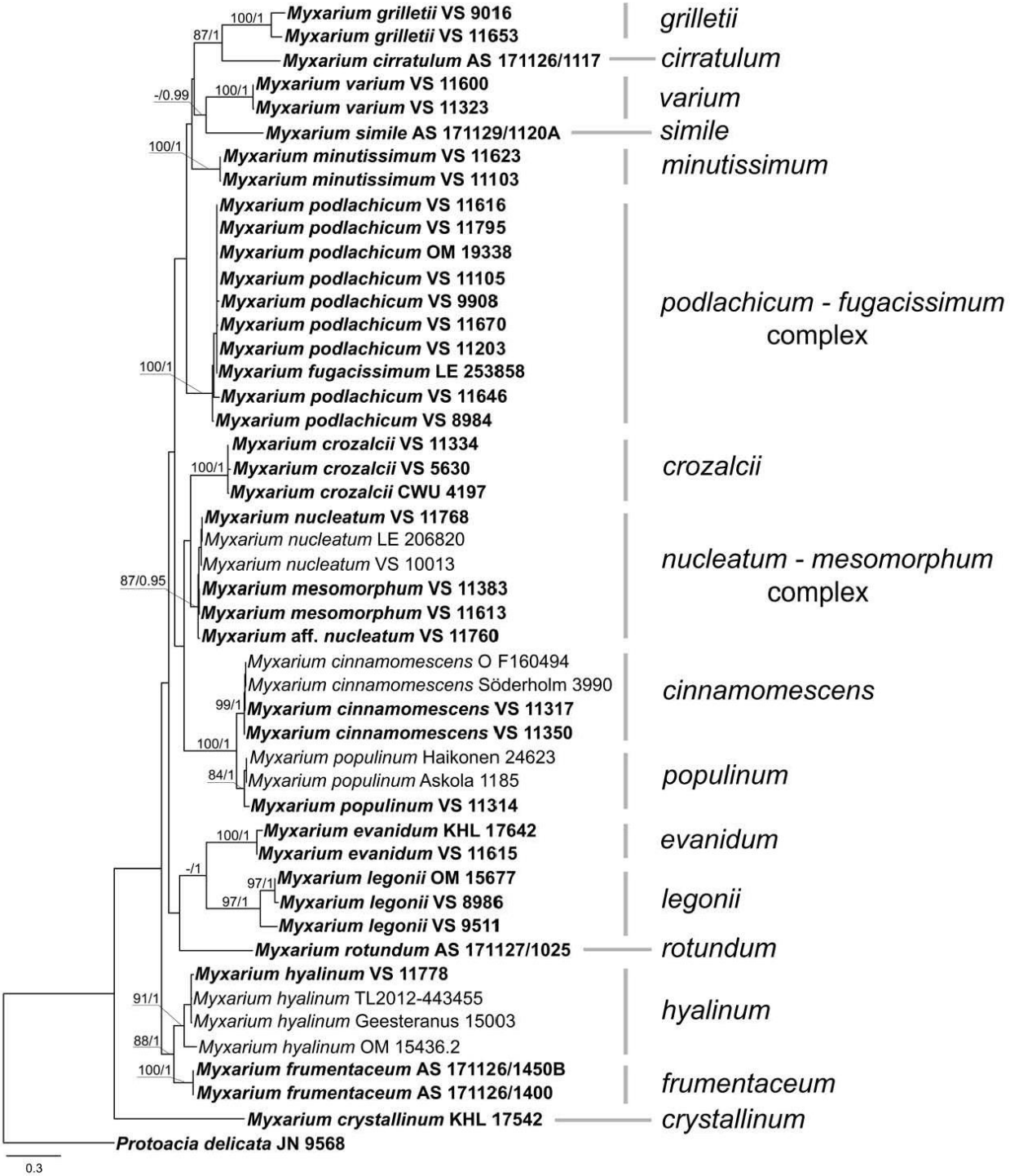

Fig. 3. Basidiocarps of *Myxarium* spp.: a – *Myxarium cinnamomescens* (Spirin 11317); b – *M. cirratulum* (Savchenko 171126/1117); c – *M. crozalcii* (Spirin 12043); d – *M. crystallinum* (Larsson 17542, scale bar = 0.5 mm); e – *M. frumentaceum* (Savchenko 171126/1400); f – *M. fugacissimum* (Spirin 12486); g – *M. grilletii* (Spirin 11653); h – *M. grilletii* (Spirin 9016). Scale bar = 10 mm.

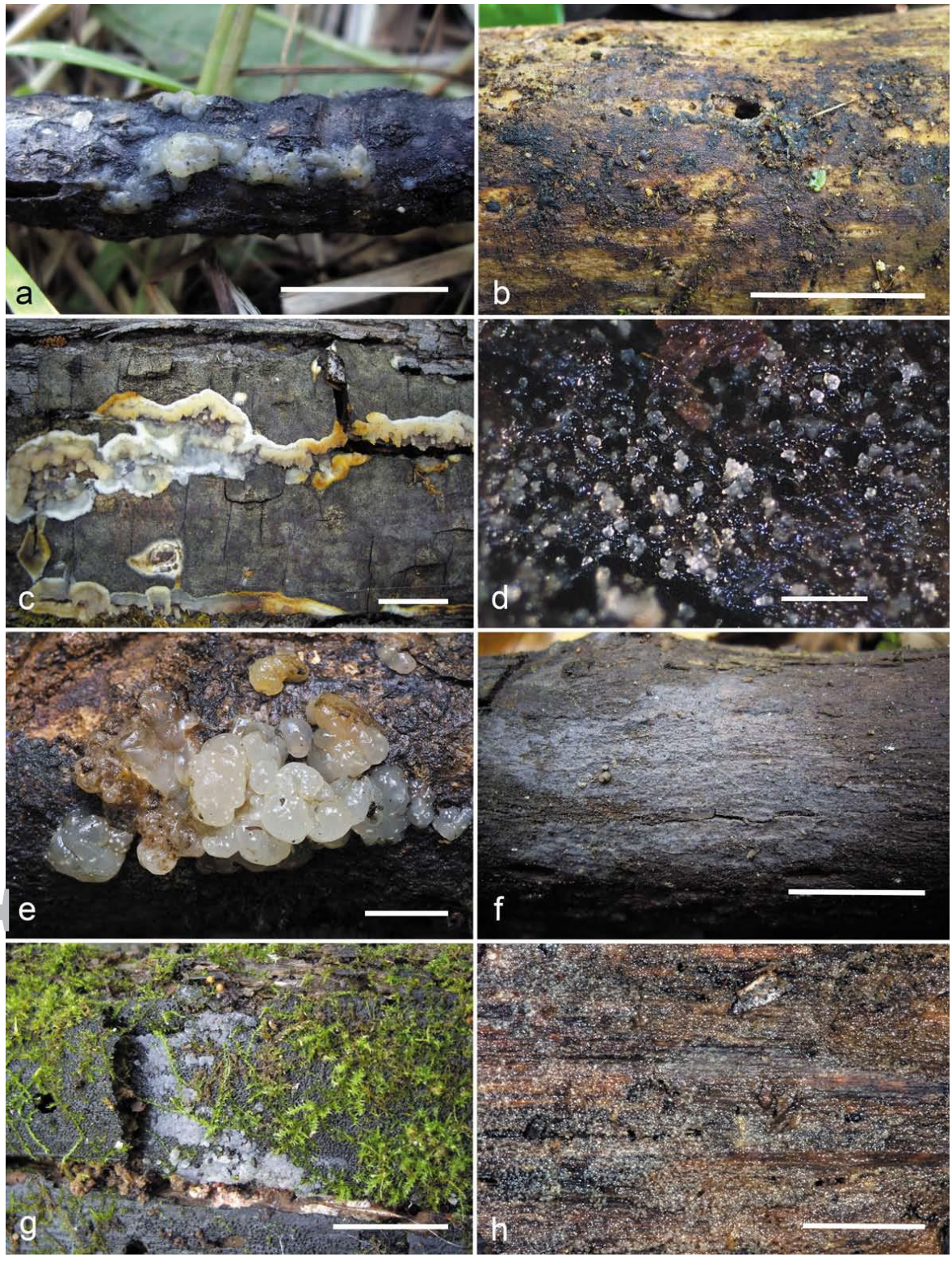

Fig. 4. Basidiocarps of *Myxarium* spp.: a – *M. legonii* (Spirin 8986); b – *M. mesomorphum* (Spirin 11613); c – *M. nucleatum* (Spirin 11768); d – *M. podlachicum* (Spirin 11670); e – *M. populinum* (Spirin 12208); f – *M. rotundum* (Savchenko 171127/1025); g – *M. simile* (Savchenko 171129/1120A); h – *M. varium* (Spirin 12008). Scale bar = 5 mm.

Fig. 5. Basidiocarps: a – *Gelacantha pura* (LE 254018); b – *Hydrophana sphaerospora* (Spirin 11779); c – *Protoacia delicata* (Nordén 9568); d – *Protodontia subgelatinosa* (Spirin 11644). Scale bar = 10 mm.

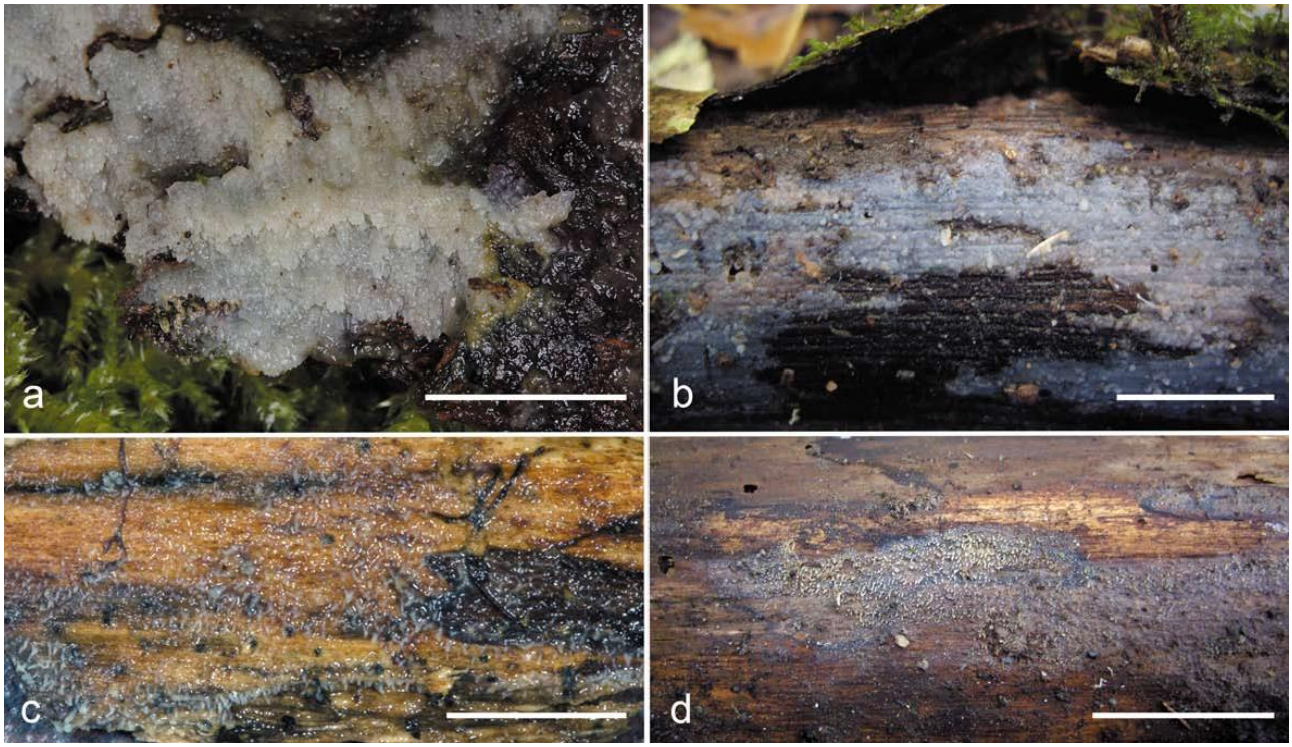

Fig 6. Basidiospores: a – *Gelacantha pura* (LE 254018); b – *Hydrophana sphaerospora* (Spirin 11133); c – *Myxariellum concinnum* (Spirin 8393c); d – *M. tenerum* (Spirin 8685); e – *Ofella glaira* (Spirin 11809); f – *Protoacia delicata* (Spirin 4615); g – *Protodontia africana* (Savchenko 171126/1104); h – *P. insularis* (Ryvarden 49417); i – *P. subgelatinosa* (Miettinen 13489). Scale bar = 10 µm.

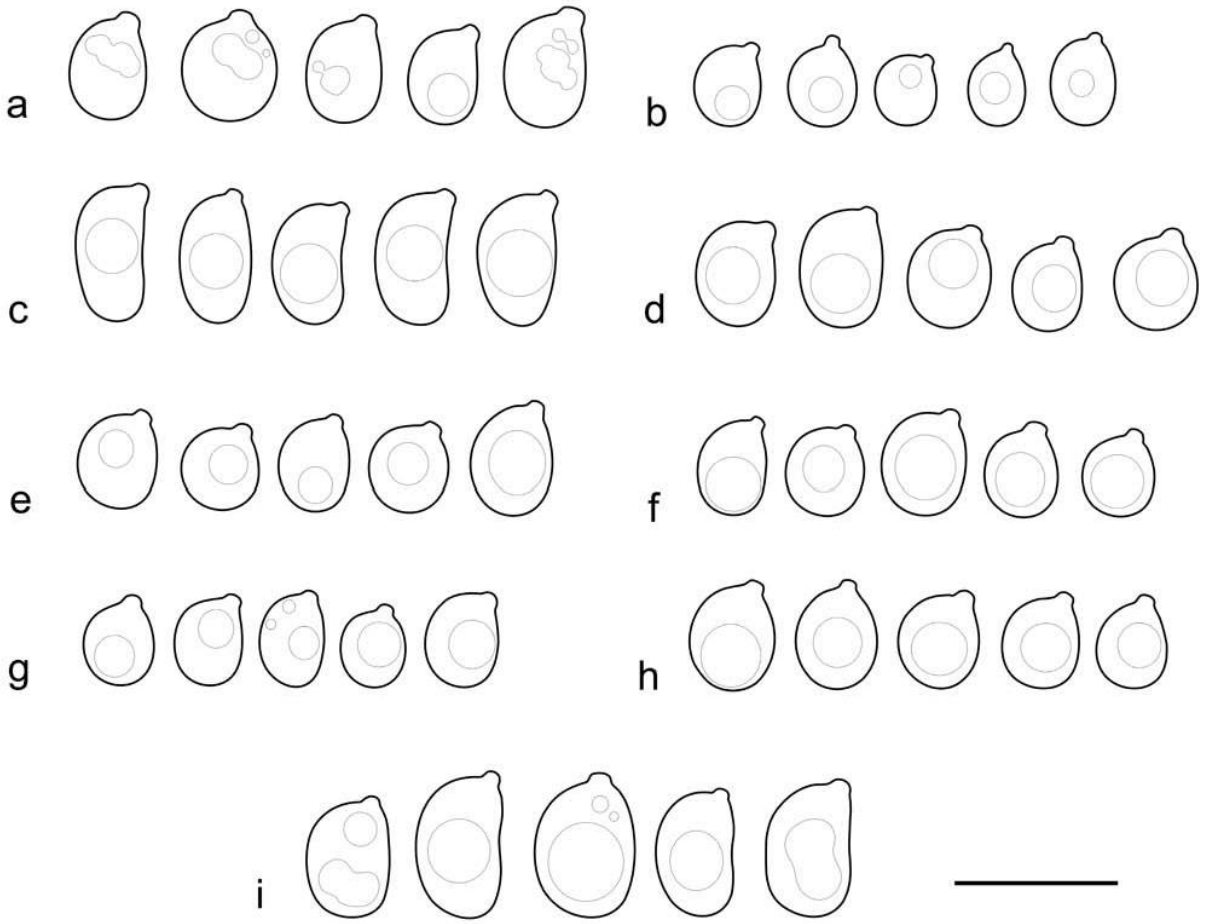

Fig. 7. Basidiospores: a – *M. cinnamomescens* (Spirin 11317); b – *M. cirratulum* (Savchenko 171126/1117); c – *M. crozalcii* (Spirin 11334); d – *M. crystallinum* (Larsson 17542); e – *M. evanidum* (Spirin 11615); f – *M. frumentaceum* (Savchenko 171126/1400); g – *M. grilletii* (Spirin 11653), h – *M. grilletii* (Spirin 9016); i – *M. fugacissimum* (LE 253858); j – *M. legonii* (Spirin 8986); k – *M. mesomorphum* (Spirin 11383); l – *M. minutissimum* (Trichies 03081); m – *M. podlachicum* (lectotype of *Sebacina podlachica*); n – *M. rotundum* (Savchenko 171127/1025); o – *M. simile* (Savchenko 171129/1120A); p – *M. varium* (Trichies 08379). Scale bar = 10 µm.

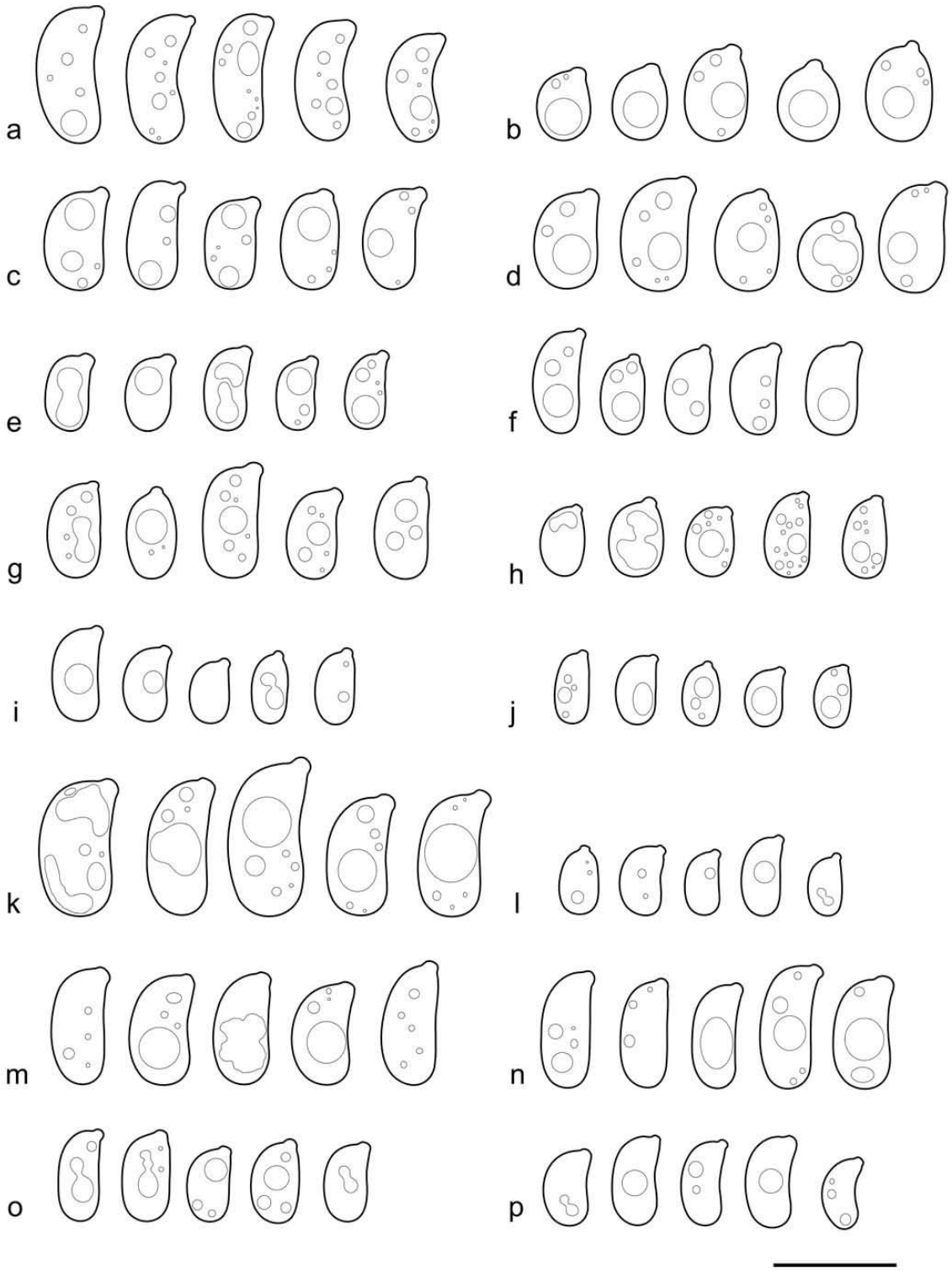

Fig. 8. Hyphae, basidia and basidiospores of *H. sphaerospora* (Spirin 11622). Scale bar = 10 µm.

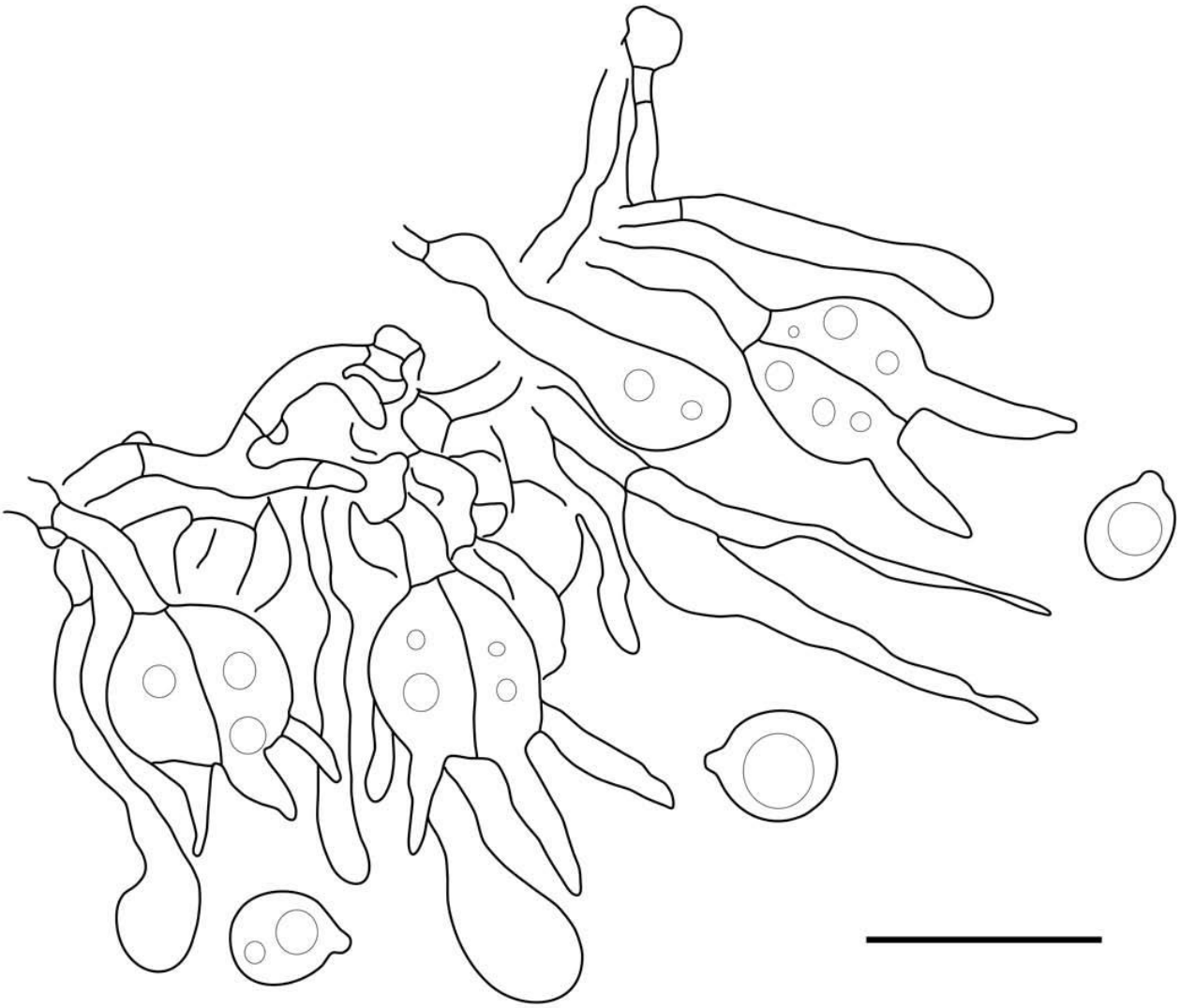

Fig. 9. Hyphae, hymenial cells and basidiospores of *M. concinnum* (Spirin 8393c). Scale bar = 10 µm.

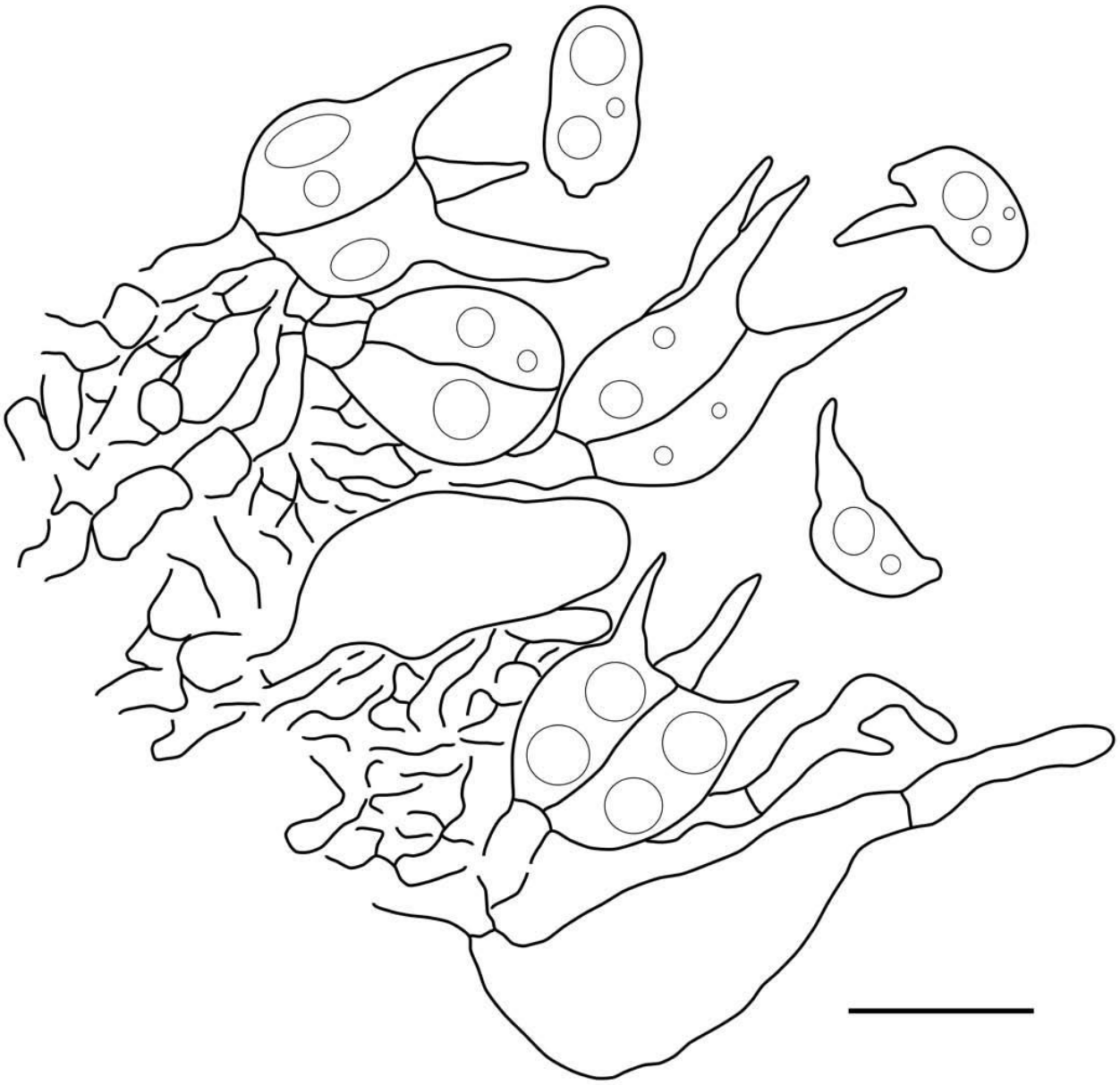

Fig. 10. Subicular hyphae, subhymenial hyphae, hymenial cells and basidiospores of *M. crozalcii* (Spirin 9334). Scale bar = 10 µm.

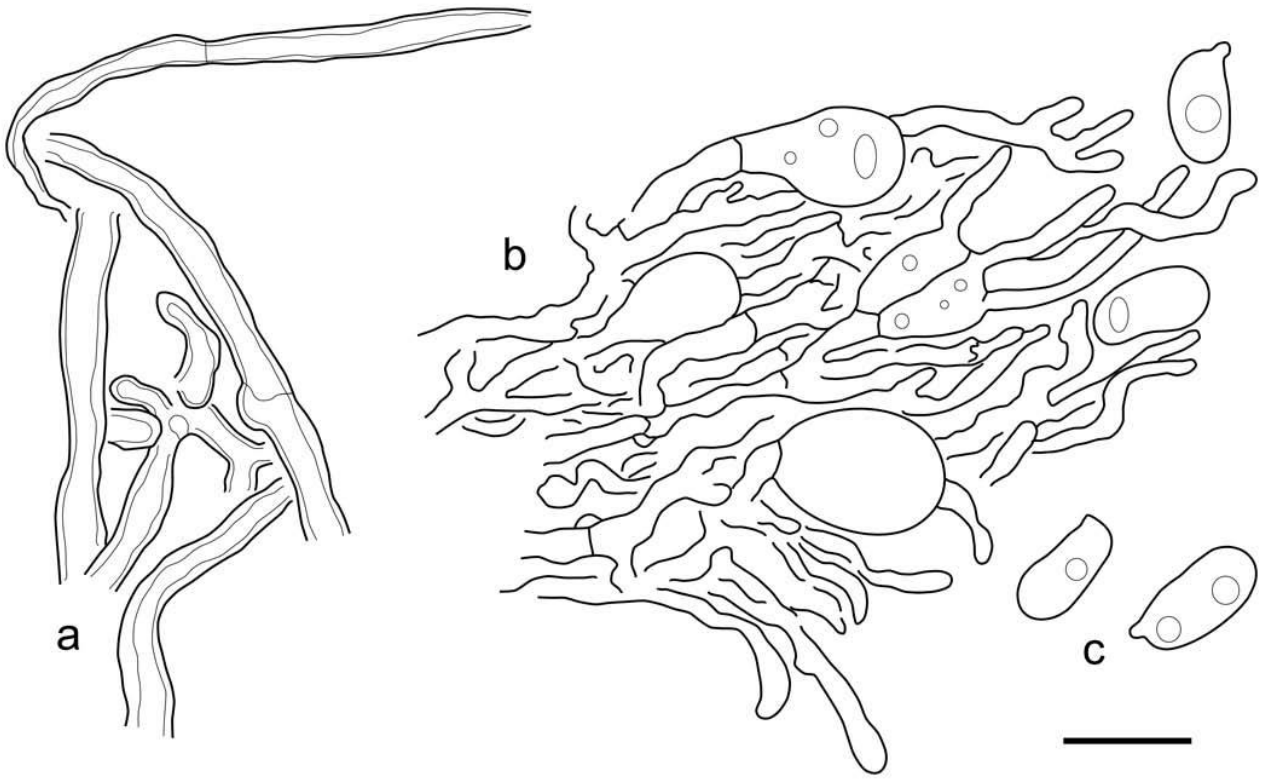

Fig. 11. Hyphae, hymenial cells and basidiospores of *M. minutissimum* (Spirin 11100). Scale bar = 10 µm.

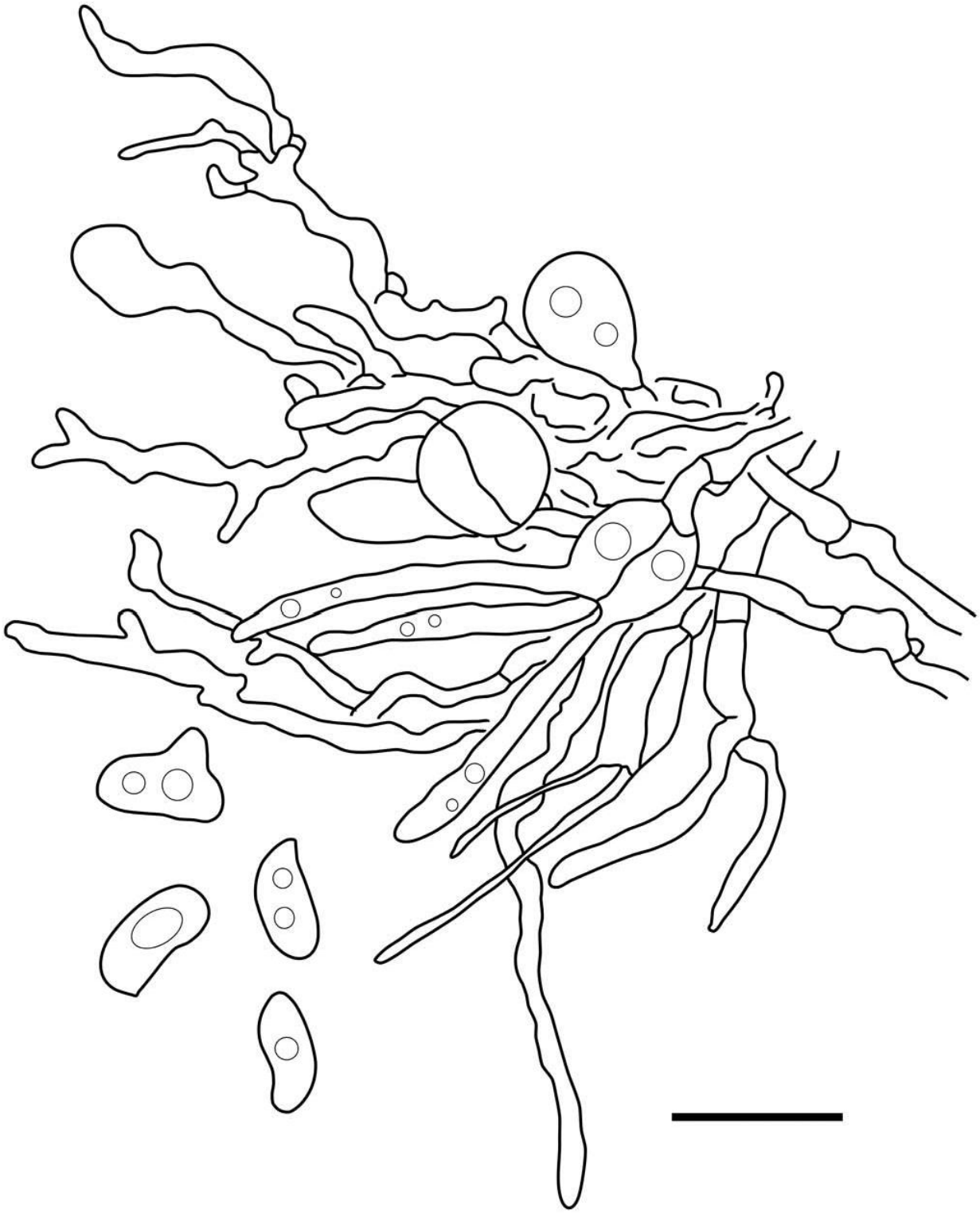

Fig. 12. Subicular hyphae, subhymenial hyphae, hymenial cells and basidiospores of *M. varium* (Trichies 08379). Scale bar = 10 µm.

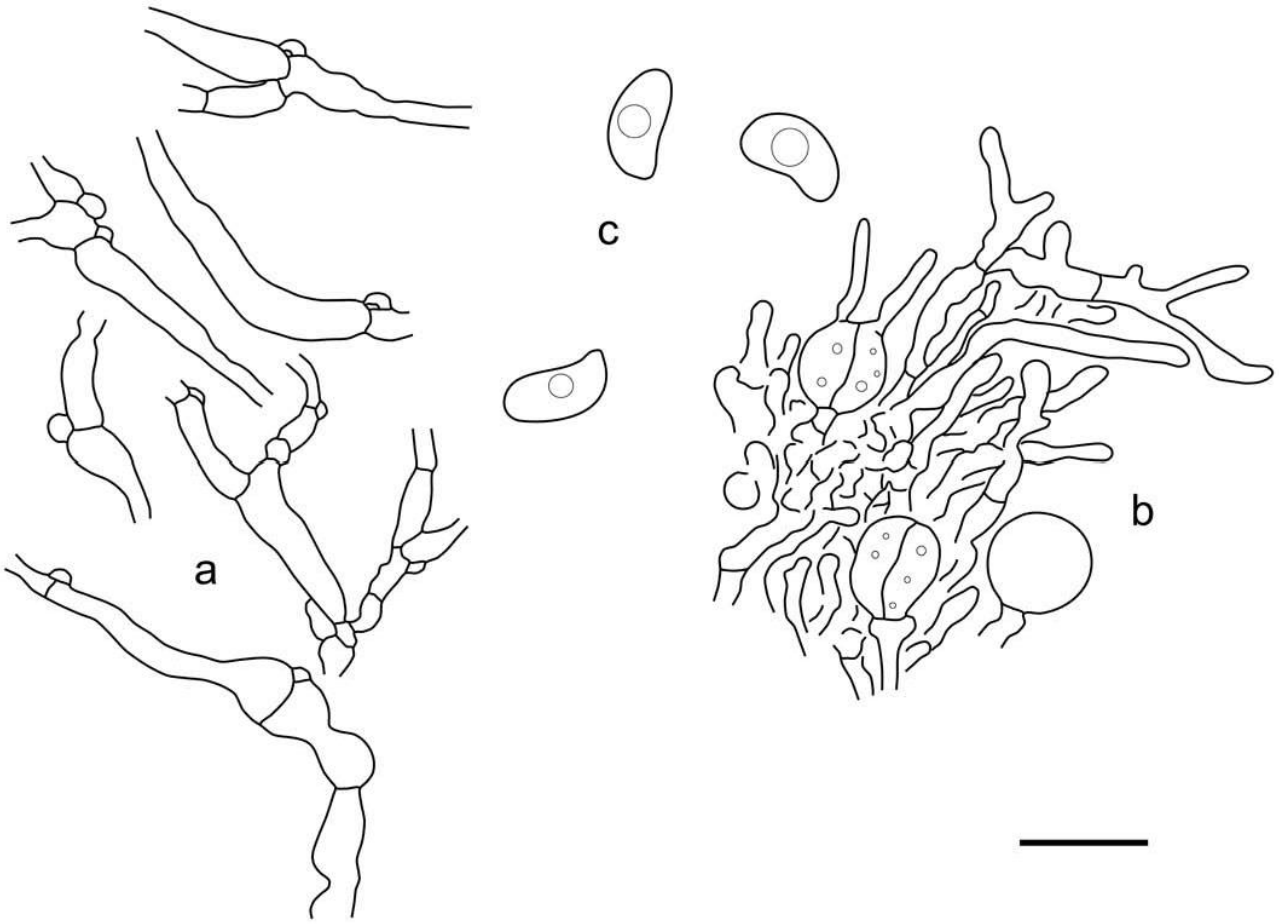

Fig. 13. Hyphae, basidia and basidiospores of *O. glaira* (Spirin 11809). Scale bar = 10 µm.

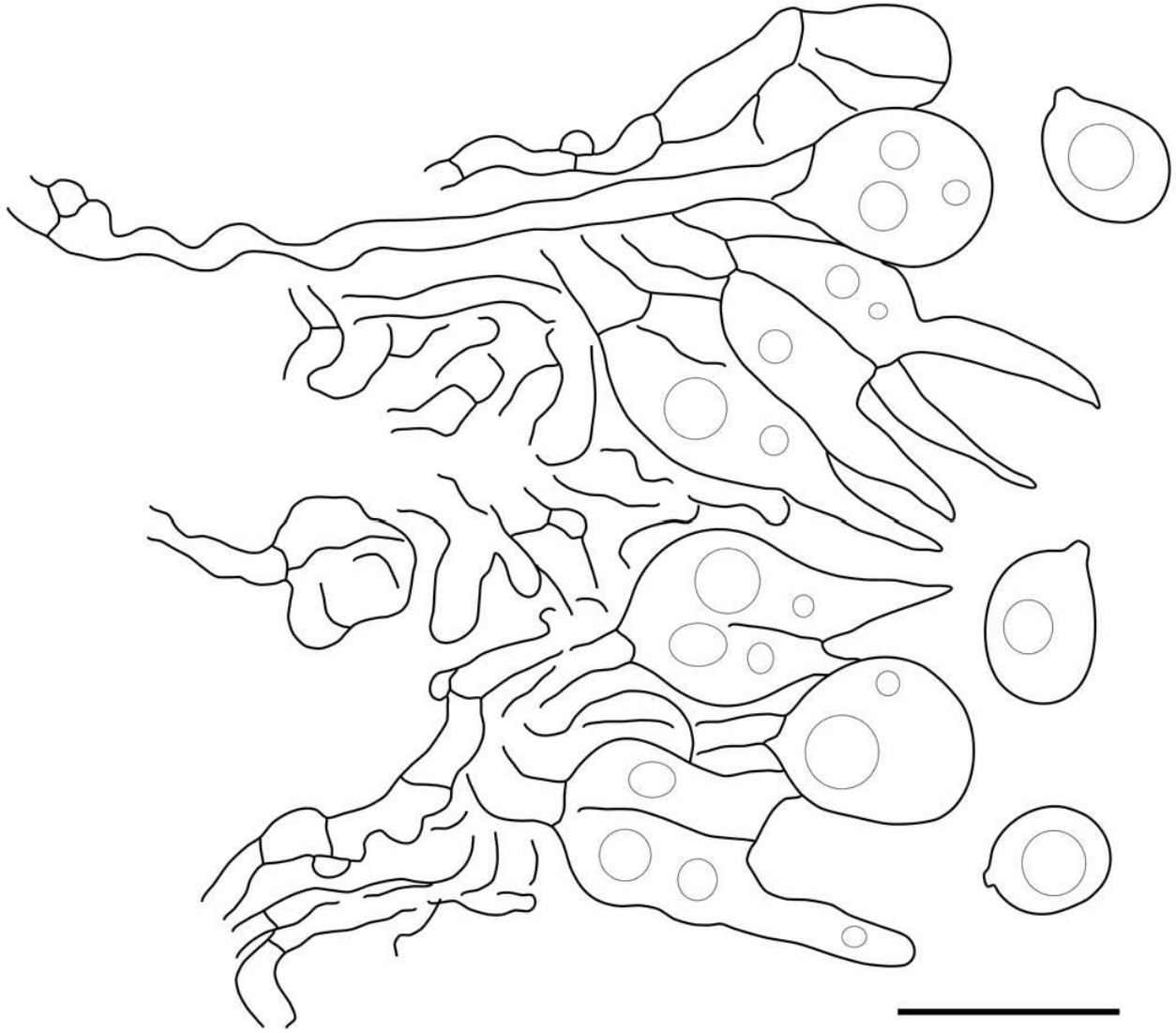

Fig. 14. Hyphae, hymenial cells and basidiospores of *P. delicata* (Spirin 4615). Scale bar = 10 µm.

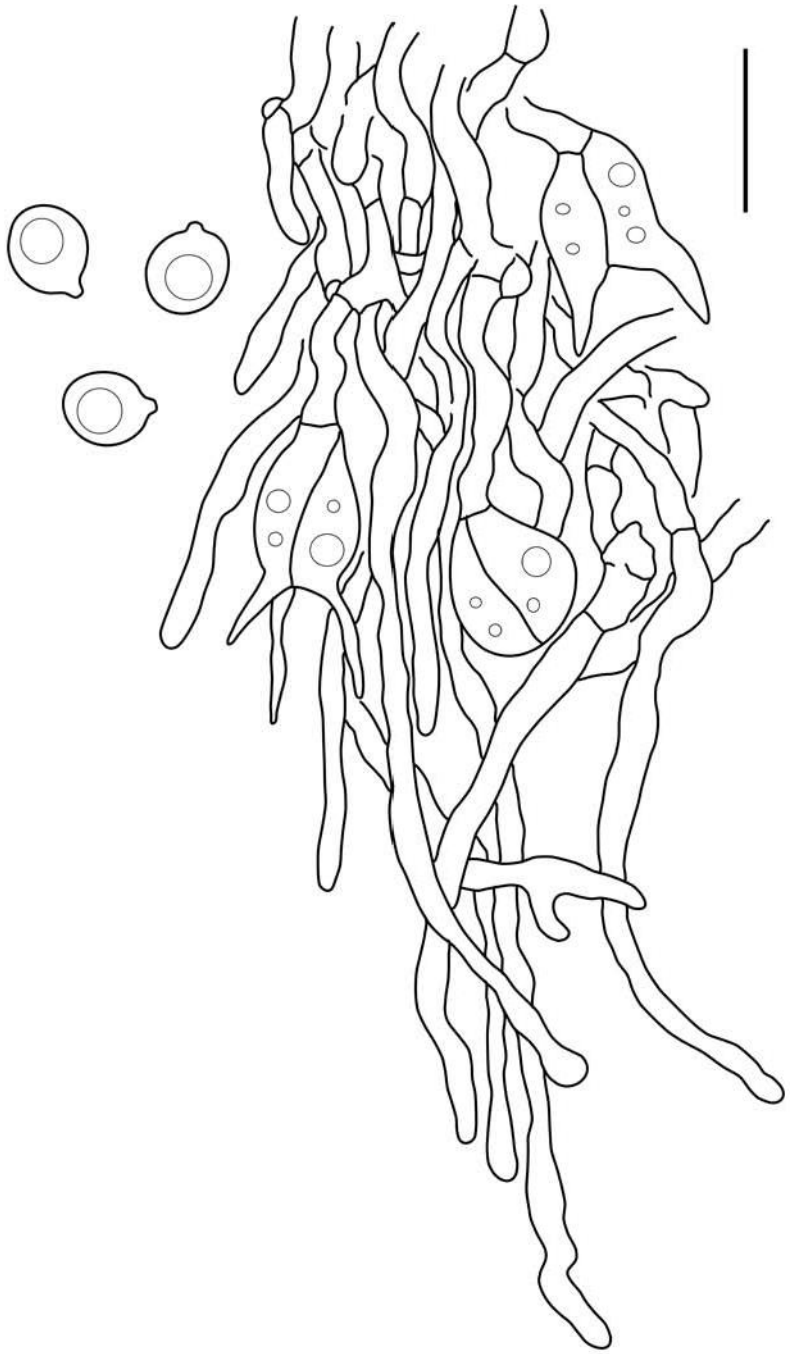

Table Legend

Table 1. Sequences used in the present study
(sequences generated for the study are given in bold faces)

Species	Specimen / herbarium	Country of origin	Host	GenBank number	
				nrLSU	nrITS
Aporpium caryae	OM 14774	US	*Populus* sp.	JX044145	JX044145
A. caryae	WD 2207	JP	-	AB871730	AB871751
Amphistereum leveilleanum	Lentz FP-106715	US	*Carya aquatica?*	KX262168	KX262119
Amphistereum schrenkii	Burdsall 8476	US	*Prosopis juliflora*	KX262178	KX262130
Auricularia mesenterica	FO 25132	DE	-	AF291292	AF291271
A. mesenterica	TUFC12805	JP	-	AB915191	-
Basidiodendron caesiocinereum	MW 320	DE	-	AF291293	-
Bourdotia galzinii	OM 15900.4	ES	conifer	MG757511	MG757511
Ductifera sucina	Wells 2155	US	-	AY509551	AY509551
Eichleriella crocata	TAAM 101077	RU	*Acer mono*	KX262147	KX262100
Eichleriella leucophaea	LE 303261	RU	*Padus avium*	KX262161	KX262111
Elmerina cladophora	OM 14314	ID	*Pterocarpus indicus (?)*	MG757509	MG757509
Elmerina sclerodontia	OM 16431	MY	*hardwood*	MG757512	MG757512
Exidia candida	VS 8450	US	*Alnus rubra*	KY801900	KY801875
E. candida	O F160269	NO	*Tilia cordata*	KY801897	KY801872
Exidia thuretiana	VS 11185	NO	*Ulmus glabra*	KY801914	KY801889
E. thuretiana	VS 9999	FI	*Ribes nigrum*	KY801905	KY801878
Exidiopsis effusa	OM 19136	FI	*Padus avium*	KX262193	KX262145
Exidiopsis grisea	RK 162	DE	-	AF291328	AF291281
Gelacantha pura	LE 254018	RU-KC	*Abies obovata*	**MK098930**	**MK098882**
Heterochaetella brachyspora	RJB 13295	-	-	-	AY509552
Heteroradulum deglubens	LE 38182	SE	hardwood	KX262162	KX262112
Heteroradulum kmetii	DAOM 145605	CA	*Populus* sp.	KX262183	KX262135
Hirneolina hirneoloides	USJ 55480	CR	-	AF291334	AF291283
Hyalodon antui	Niemelä 6389	CN	*Abies* sp.	MG735424	MG735416
Hyalodon piceicola	VS 2689	RU	*Picea abies*	MG735422	MG735414
H. piceicola	VS 11063	NO	*P. abies*	MG735423	MG735415
Hydrophana sphaerospora	VS 11133 (O)	NO	*Sorbus aucuparia*	**MK098931**	**MK098883**
H. sphaerospora	VS 11622 (O)	NO	*Alnus incana*	**MK098932**	**MK098884**
Mycostilla vermiformis	VS 11621	NO	*Pinus sylvestris*	MG857098	MG857093
M. vermiformis	VS 11330	RU	*P. abies*	MG735425	MG735417
Myxariellum concinnum	VS 8393c (H)	US-WA	*Thuja plicata*	**MK098933**	**MK098885**
Myxariellum tenerum	VS 8685 (H)	US-WA	*Picea engelmannii*	**MK098934**	**MK098886**
Myxarium cinnamomescens	VS 11317 (H)	RU-NIZ	*T. cordata*	**MK098935**	**MK098887**
M. cinnamomescens	VS 11350 (H)	RU-NIZ	*T. cordata*	**MK098936**	**MK098888**
M. cinnamomescens	O F160494	NO	*Populus tremula*	-	KY801882
M.cinnamomescens	Söderholm 3990	FI	*P. avium*	-	KY801886
Myxarium cirratulum	AS 171126/1117 (H)	KE	hardwood	-	**MK098979**
Myxarium crozalcii	VS 5630 (H)	RU-KHA	*Syringa amurensis*	**MK098937**	**MK098889**
M. crozalcii	VS 11334 (H)	RU-NIZ	*T. cordata*	**MK098938**	**MK098890**
M. crozalcii	CWU 4197	UA	*Betula pendula*	**MK098939**	**MK098891**
Myxarium crystallinum	KHL 17542 (O)	NO	*U. glabra*	**MK098940**	**MK098892**
Myxarium evanidum	KHL 17642 (O)	NO	decayed wood	**MK098941**	**MK098893**
M. evanidum	VS 11615 (O)	NO	*U. glabra*	-	**MK098894**
Myxarium frumentaceum	AS 171126/1400 (H)	KE	hardwood	**MK098975**	**MK098981**

M. frumentaceum	AS 171129/1350 (H)	KE	hardwood	**MK098974**	-
M. frumentaceum	AS 171126/1450B (H)	KE	hardwood	-	**MK098980**
Myxarium fugacissimum	LE 253858	RU-KC	*Fagus sylvatica*	**MK098942**	**MK098895**
M. fugacissimum	LE 262916	RU-PRI	hardwood	**MK098943**	-
M. granulum	USJ 54532	CR	-	AF291348	-
Myxarium grilletii	VS 9016 (H)	CA-AB	*Populus alba*	**MK098944**	**MK098896**
M. grilletii	VS 11047 (O)	NO	*U. glabra*	**MK098946**	-
M. grilletii	VS 11653 (O)	NO	*P. tremula*	**MK098945**	**MK098897**
M. grilletii	RoKi 218	DE	-	AF291349	-
Myxarium hyalinum	VS 11778 (O)	NO	*T. cordata*	-	**MK098898**
M. hyalinum	OM 15436.2	DE	hardwood	KY801913	KY801887
M. hyalinum	TL2012-443455	DK	*T. cordata*	-	KY801880
M. hyalinum	Geesteranus 15003	NL	*Acer* sp.	-	KY801881
Myxarium legonii	VS 8986 (H)	CA-AB	*P. alba*	**MK098947**	**MK098899**
M. legonii	VS 9511 (H)	RU-NIZ	*U. glabra*	-	**MK098900**
M. legonii	OM 15677 (H)	US-NY	decayed wood	**MK098948**	**MK098901**
Myxarium mesomorphum	VS 11613 (O)	NO	*Sorbus* sp.	-	**MK098902**
M. mesomorphum	VS 11383 (H)	RU-LEN	*T. cordata*	**MK098949**	**MK098903**
Myxarium mesonucleatum	USJ 55354	CR	-	AF291350	-
Myxarium minutissimum	VS 11103 (O)	NO	*Acer platanoides*	**MK098950**	**MK098904**
M. minutissimum	VS 11623 (O)	NO	*U. glabra*	**MK098951**	**MK098905**
Myxarium nucleatum	VS 11768 (O)	NO	*T. cordata*	-	**MK098906**
M. nucleatum	LE 206820	RU	*T. cordata*	KY801894	KY801869
M. nucleatum	VS 10013	NO	*T. cordata*	-	KY801879
Myxarium aff. *nucleatum*	VS 11760 (O)	NO	*Ilex aquifolium*	-	**MK098907**
Myxarium podlachicum	VS 8984 (H)	CA-AB	*P. alba*	**MK098952**	**MK098908**
M. podlachicum	OM 19338 (H)	FI	*Betula pubescens*	**MK098953**	**MK098909**
M. podlachicum	VS 11105 (O)	NO	*P. tremula*	**MK098954**	**MK098910**
M. podlachicum	VS 11203 (O)	NO	*A. incana*	**MK098955**	**MK098911**
M. podlachicum	VS 11616 (O)	NO	*U. glabra*	**MK098956**	**MK098912**
M. podlachicum	VS 11646 (O)	NO	*A. incana*	**MK098957**	**MK098913**
M. podlachicum	VS 11670 (O)	NO	*Corylus avellana*	**MK098958**	**MK098914**
M. podlachicum	VS 11795 (O)	NO	*Ulmus* sp.	-	**MK098915**
M. podlachicum	VS 11510 (H)	RU-LEN	*B. pubescens*	**MK098960**	-
M. podlachicum	VS 9908 (H)	RU-NIZ	*Quercus robur*	**MK098959**	**MK098916**
Myxarium populinum	VS 11314 (H)	RU-NIZ	*P. tremula*	**MK098961**	**MK098917**
M. populinum	Haikonen 24623	FI	*P. tremula*	KY801910	KY801883
M. populinum	Askola 1185	FI	*P. tremula*	-	KY801885
Myxarium rotundum	AS 171127/1025 (H)	KE	hardwood	**MK098976**	**MK098982**
Myxarium simile	AS 171129/1120A (H)	KE	hardwood	**MK098977**	**MK098983**
Myxarium subhyalinum	MW 527	DE	-	AF291352	-
Myxarium varium	VS 11600 (O)	NO	*A. incana*	**MK098962**	**MK098918**
M. varium	VS 11323 (H)	RU-NIZ	*B. pubescens*	**MK098963**	**MK098919**
Myxarium sp.	FO 35744	DE	-	AF291353	-
Ofella glaira	VS 11809 (O)	NO	*P. abies*	**MK098964**	**MK098920**
Protoacia delicata	JN 9568 (O)	NO	*P. abies*	**MK098965**	**MK098921**
P. delicata	VS 7824 (H)	RU-KHA	*Picea ajanensis*	**MK098966**	**MK098922**
P. delicata	VS 4615 (H)	RU-LEN	*P. abies*	**MK098967**	**MK098923**
Protodaedalea foliacea	OM 13054	ID	hardwood	MG757507	MG757507
Protodaedalea hispida	VS 5139	RU	*Tilia amurensis*	MG757510	MG757510
P. hispida	WD 548	JP	-	AB871749	AB871768
Protodontia africana	AS 171126/1104 (H)	KE	hardwood	**MK098973**	**MK098978**

Protodontia insularis	LR 49417 (H)	SH-HL	hardwood	**MK098968**	**MK098924**
Protodontia subgelatinosa	OM 14934.1 (H)	FI	*A. incana* / *Salix caprea*	-	**MK098925**
P. subgelatinosa	VS 11038 (O)	NO	*A. incana*	**MK098969**	**MK098926**
P. subgelatinosa	VS 11079 (O)	NO	*B. pubescens*	**MK098970**	**MK098927**
P. subgelatinosa	OM 13489 (H)	NO	*B. pubescens*	**MK098971**	**MK098928**
P. subgelatinosa	VS 5123 (H)	RU-KHA	*Abies nephrolepis*	**MK098972**	**MK098929**
Protohydnum cartilagineum	SP467240	BR	hardwood	MG735426	MG735419
Protomerulius sp.	OM 14402.1	ID	hardwood	MG757508	MG757508
Protomerulius sp.	O 19171	-	-	JQ764649	JX134482
Pseudohydnum gelatinosum	F14063	-	-	-	AF384861
P. gelatinosum	MW 298	-	-	DQ520094	DQ520094
Sclerotrema griseobrunneum	VS 7674	RU	*Alnus fruticosa*	KX262188	KX262140
S.griseobrunneum	Niemela 2722	CA	*Alnus crispa*	KX262192	KX262144
Sistotrema brinkmannii	Isolate 236	-	-	JX535170	JX535169
Stypellopsis farlowii	VS 8254	US	*Tsuga heterophylla*	MG857100	MG857094
S. farlowii	Larsson 12337	US	decayed wood	MG857099	MG857095
Stypellopsis hyperborea	VS 11066	NO	*P. abies*	MG857102	MG857096
S. hyperborea	J. Nordén 9751	NO	*P. abies*	MG857101	MG857097
Tremellochaete japonica	LE 303446	RU	hardwood	KX262160	KX262110
Tremiscus helvelloides	MW 337	-	-	DQ520100	DQ520100
Uncultured Basidiomycota	Clone 6d1	US	environmental sample	-	JQ247543
Uncultured Basidiomycota	Clone 6d5	US	environmental sample	-	JQ247544